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A PRELIMINARY ACCOUNT OF A COLONY OF GREY SEALS *HALICHOERUS GRYPUS* (FAB.) IN THE SOUTHERN INNER HEBRIDES

BY

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[Accepted 14th April 1959]

(With 2 plates and 19 figures in the text)

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INTRODUCTION

The breeding colony of grey seals on the islands centred on Oronsay in the Southern Hebrides has never been described. It is probably not a particularly large group of animals nor is the area concerned extensive, but it is important, being the most southerly of the Scottish colonies.

The breeding colony nearest to it is that on the Treshnish Isles described to some extent by Darling (1939, 1947). This is 35 miles away to the N.W. but, as will be shown, has several features in common with the present colony. To the south the colonies in the southern Irish Sea appear to be the nearest, although the occasional pup known to be born on Rathlin Island off the Antrim coast might be quoted.

Little information was available to enable us to determine the best period for observation. Mr John Mathias had visited one of the islands in the 1930s when making a documentary film. He kindly gave us valuable help from his experience. We are also greatly indebted to Lord Strathcona and Mount Royal,

laird of Colonsay, for his encouragement and assistance, to Mr and Mrs Andrew McNeil of Oronsay Farm for much practical help and kindness and to Mr A. MacAlister for transport in not always the best of weather. Our thanks are also due to Mr Mackenzie for the loan of a boat and out-board motor, which enabled us to visit the other islands when the weather permitted.

Two visits have been made, one in 1956 from 19th September to 5th October and the other in 1957 from 3rd September to 26th September, thus providing an overlap. In both years Eilean nan Ron was made the base, camping on the northern third of the island (Fig. 3). Fresh water was obtainable on this portion in a wet year (1957) and on the central portion in the drier 1956.

Fig. 1.—Oronsay and the surrounding islands.

A short break in observations occurred in 1956 from 27th to 29th September when, going to Oronsay for further stores, our return was prevented by a gale. In 1957 it was our intention to separate and for one to stay on the nearby island, Eilean Ghaoidmeal for at least ten days. Bad weather however prevented us from reaching the island until it was too late to make such a prolonged visit worth while. Thus in each year this island was visited twice only for purposes of census and the ringing of pups. It is not easy to land on the island.

In August 1957 a party of students from the Zoology Department, Imperial College, worked on Oronsay and kept records relating to the seals. On 12th

August five* of them landed on Eilean nan Ron and made a census. These records have been kindly given to us to include in the data.

The note-book containing all the field observations written up in cursive form on the same day will be deposited with the Nature Conservancy, who partly defrayed the cost of the expedition.

THE TERRAIN

Davies (1949) attributed the main characteristics of the organisation of Pembrokeshire breeding colonies to geographical features. Darling (1947, p. 224) records a linear distribution of bulls on the Treshnish Isles as due to a narrow strip of raised beach, and the chequer-board pattern of bull territories on North Rona to the gentle slope from sea-level which gives access to the turf-covered expanses of the island. One of us (Hewer, 1957) has also shown that peculiar behaviour both before and during the breeding period on Shillay is associated with the broad shell-sand beach, sand-dunes and peat-bog wallows inland. The present colony similarly can only be understood in the light of the geography of the islands.

The disposition of the islands is shown in Fig. 1. All are involved in some way but Eilean nan Ron and Eilean Ghaoidmeal are those used principally for pupping, the latter more than the former. Eilean Eoin and Carn Riobha are used to a much less extent owing to their smaller size. All these, together with numerous skerries are used for haul out before and during the breeding season. The "mainlands" of Oronsay and of Colonsay are also used for early haul-out and for a few pups. It will be convenient to consider the geographical peculiarities of Eilean nan Ron and to give comparisons with Eilean Ghaoidmeal and the other islets and skerries.

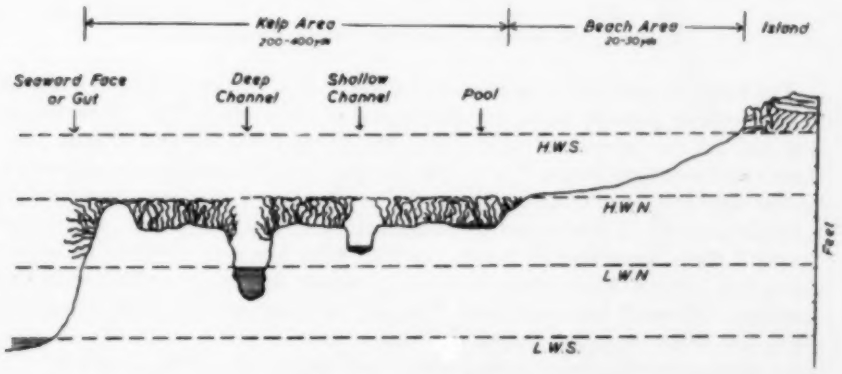


Fig. 2.—Diagrammatic section through the shore-line of Eilean nan Ron or Ghaoidmeal.

The dominant feature of the coastline of Eilean nan Ron is a "lowered beach" or erosion platform but its level, relative to the high and low water marks at both neap and spring tides is important. A diagram is shown (Fig. 2)

* R. Sturrock, J. Webster, E. E. Donahaye, J. Jones and Miss Bergazyn-Schlesinger.

of a section through the island coastline. Geologically speaking there is an erosion platform at a present elevation which leaves it between low and high water marks. Thus its very considerable extent (Fig. 3) increases the area of the island by four times at low water. Several parts are well over a quarter of a mile wide. It is profusely covered in " kelp ", with *Ascophyllum* sp. dominant. The seaward face is in most places surrounded by a ridge, which protects the beaches from the pounding Atlantic. This seaward face drops abruptly to the *Laminaria* zone. In consequence there is little difference in the total areas exposed at neaps and at springs.

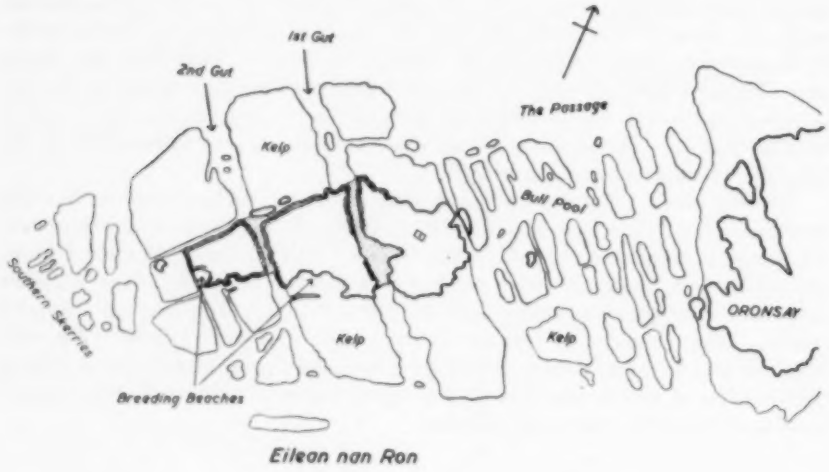


Fig. 3.—Eilean nan Ron and the Passage at low-water.

The kelp-covered platform is not uniform. It is intersected by a series of channels either parallel to or at right angles to the shore. Two of these are deep and cut the permanent land of the island into three sections at high tide. These two have been called " guts " by us (Fig. 3). The others are of varying depths and have been termed " channels ". The flatter areas are also variable in height so that at low water there remain extensive " lagoons " or smaller " pools " while a number of ridges, varying from three to six feet in height above the general level, may be seen, generally running parallel with the shoreline. These " lagoons " and " pools " are present at both neap and spring low tides, only the " channels " and " guts ", which extend to the sea, being affected by the lower water levels of the spring tides (Figs. 3 and 4).

The tides are remarkably small, those of neap quite exceptionally so (average 4 feet). As the height of spring tides are about 12 feet only, the difference between H.W.S. and H.W.N. is about equal to that between H.W.N. and L.W.N. The general level of the kelp-covered platform is about half-way between H.W.N. and L.W.N. (Fig. 2).

This results in the kelp-covered area being exposed for about eight hours

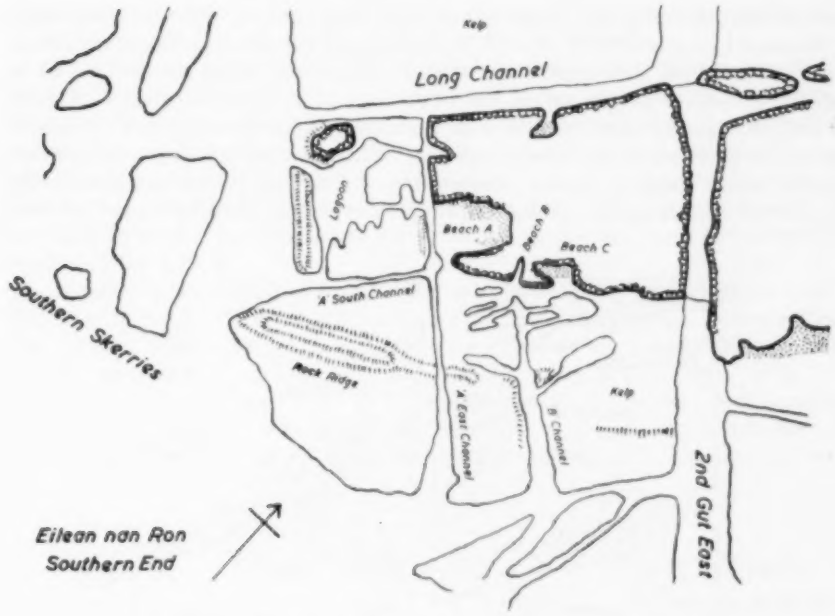


Fig. 4.—Southern end of Eilean nan Ron, showing the general configuration of the erosion platform, the lagoons and channels and the positions of Beaches, A, B and C.

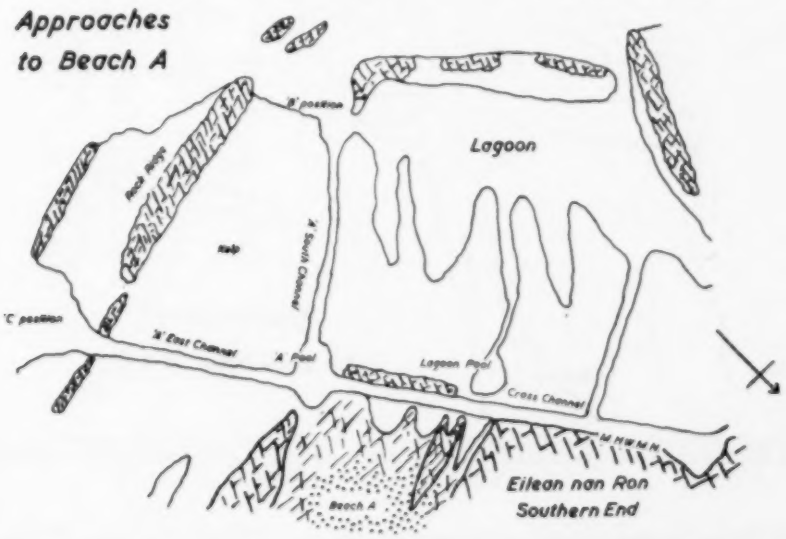


Fig. 5.—The approaches to Beach A. This sketch-map should be used in conjunction with Figs. 15 and 19 A and B.

for all tides, or for sixteen hours out of every twenty-four. The *relatively* large difference between H.W.N. and H.W.S. also results in a well defined beach zone on the landward side wherever the character of the rocks permits. This is also particularly noticeable on the east coast of Eilean Ghaoidmeal (Fig. 8) which is a gently sloping surface of vertically disposed strata well protected from the open sea by an outer ridge (reef at high water). There are a number of narrowing shelly or sandy beaches disposed around Eilean nan Ron, fewer on Eilean Ghaoidmeal. These are frequently encumbered by masses of dead

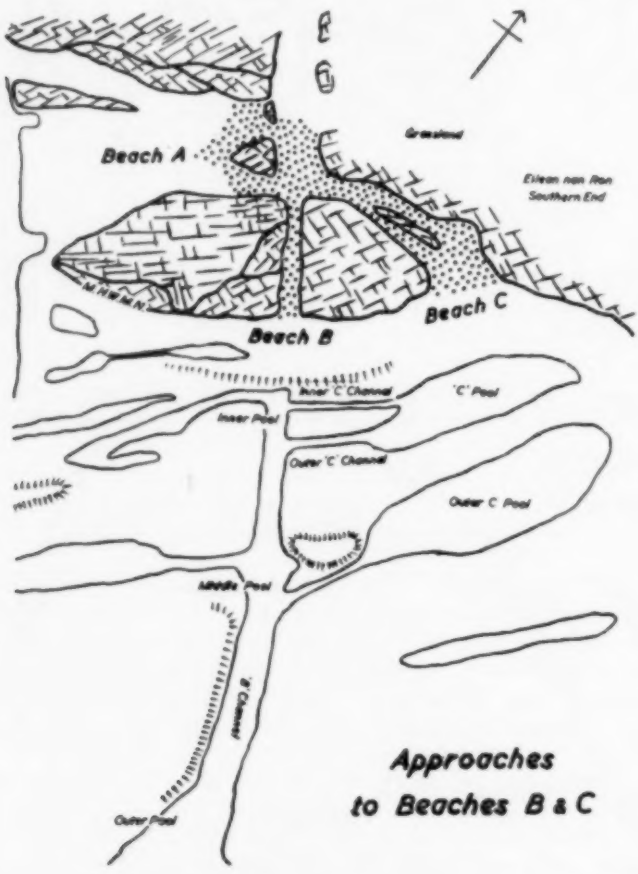


Fig. 6.—The approaches to Beaches B and C. This sketch-map should be used in conjunction with Figs. 13, 14, 16, 17 and 18.

and rotting seaweeds. It will be seen therefore that, taking all these features into consideration, the true landward beaches, washed only by spring tides, are separated from the open sea for two-thirds of the time by a wide area of

kelp-covered " land ". The only possible permanent or even semi-permanent connections with the sea are by channels, pools and lagoons.

Particular attention is directed to the southern end of Eilean nan Ron (Fig. 4). Here the presence of four beaches in close proximity, together with a number of inter-communicating channels, lagoons and pools, produces a complex terrain which has been the subject of considerable observation by us and to which repeated references will be made. In the course of describing the activities of the colony a number of the place-names indicated on this map will be used. Further names are shown on the sketch plans of individual beaches (Figs. 4 to 6).

Attention is also directed to the maze of skerries lying between Eilean nan Ron and Oronsay. This extensive area, called by us the Passage, owing to the considerable tidal flow which passes through it, is completely covered at H.W.S. except for one small skerry with a shelly beach in the centre. (Fig. 7). It is effectively covered at H.W.N. although in any wind or swell it is a mass of breakers. At the lowest L.W.S. of April and September it is possible to walk across from Oronsay to Eilean nan Ron. Its general characteristics are

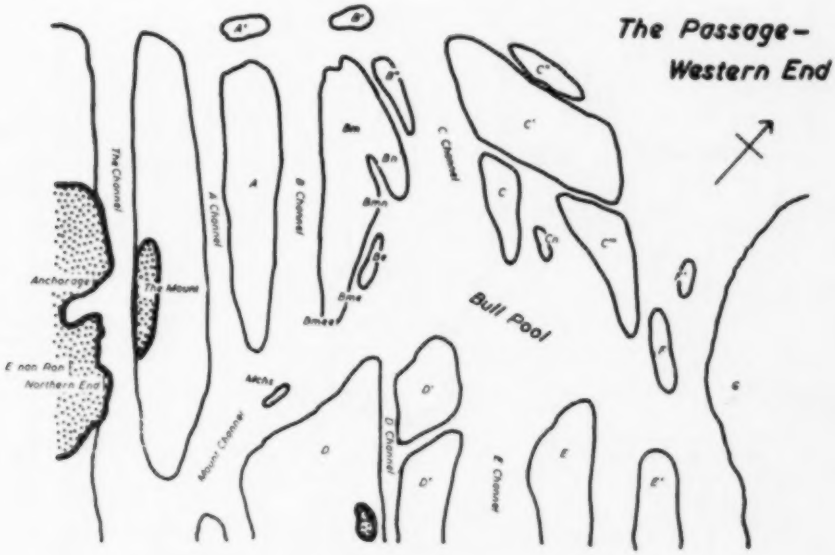


Fig. 7.—Sketch-map of the skerries in the Passage surrounding Bull Pool to be used in conjunction with Figs. 12 A, B, C and D.

similar to those of the kelp-covered area around the island except that the proportion of water to " land " is greater. Two hours after H.W., sheltered water is found in all the channels and along the sides of the skerries.

None of the islands reaches a height above 50 feet. Eilean nan Ron has low cliff faces of up to 15 feet in height in a few places, but elsewhere access to the grassland is available by very gentle slopes (Fig. 4). Beaches A, B and C all join at their heads in a patch of sand which rises imperceptably into grassland (Fig. 6). On Eilean Ghaoidmeal, although the cliffs are more extensive in proportion, at least half the coastline offers no obstacle (Fig. 8). The kelp covered area around Eilean Ghaoidmeal is no more than 100 to 150 yards wide except at the southern end.

Neither island is inhabited but Eilean nan Ron is grazed by two to three dozen sheep during the summer and by about 600 barnacle geese in the late autumn and winter. Eilean Ghaoidmeal is covered in a thick tangle of grass and, in places, bracken or heather.

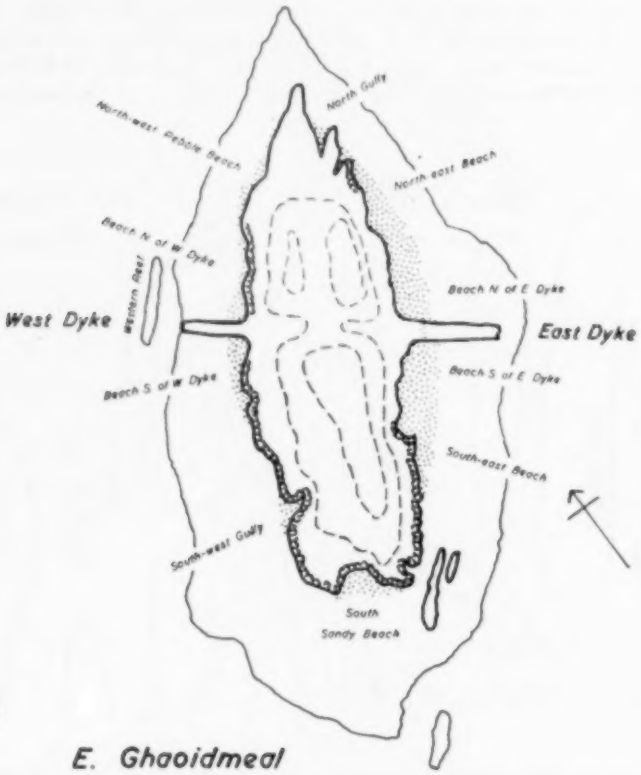


Fig. 8.—Eilean Ghaoidmeal showing the position of the breeding beaches.

Eilean Ghaoidmeal is smaller than Eilean nan Ron but rises to 45 feet on a long ridge or backbone. It is bisected by a shallow valley along a line indicated by a basaltic dyke which projects from both east and west shores cutting

them into north and south halves. (Fig 8). The beaches between H.W.N. and H.W.S. are not so isolated as on Eilean nan Ron except for a large shell-sand beach at the southern end which is cut off by cliffs to the north on both east and west sides. Elsewhere the beach is almost continuous although the western dyke is insurmountable by seals and a ridge of rock running N.N.E. separates the northern gullies from the N.E. beach. Along the N.W. coast there is an extensive raised beach sloping to a narrow kelp-covered area. Eilean Ghaoidmeal, lying in the Sound, is not subject to the same exposure as Eilean nan Ron.

Eilean Eoin (Fig. 1) although small, has a grass covered top, but only a few pups are born on it. The surrounding kelp area is used for hauling out.

Carn Riobha is little more than a large skerry but a shell sand beach among the rocks makes it suitable for breeding on a very small scale. The kelp area

TABLE 1

Censuses on Eilean nan Ron, 1956.

Date	Bulls, Cows, Juveniles	Passage	West Side	South W. Side	Beaches	East Side	Totals	Total Adults	Total	Pups	Time of Census	Time of Daylight Low Water	Springs and Neaps
20. ix	B	7	4	3	2	1	17	115	126	21	11.00–13.00 & 15.30–16.00	12.21	
	C	20	8	10	10	6	54						
	?	17	—	15	—	12	44						
	J	5	3	2	—	1	11						
22. ix	B	19	3	3	6	3	34	134	154	24	14.00 to 16.45	13.21	Spring (23. ix)
	C	10	5	15	27	11	68						
	?	23	8	1	—	—	32						
	J	18	2	—	—	—	20						
24. ix										34	No full census		
26. ix	B	2	2	2	10	2	18	87	124	40	14.45 to 17.0	15.57	
	C	6	7	7	38	11	69						
	J	7	12	8	—	10	37						
1. x	B	—	3	—	11	3	17	84	96	45*	10.00 to 11.00	09.47	Neap (29. ix)
	C	4	12	2	35	14	67						
	J	4	7	—	—	1	12						
3. x.										46	No full census		

* No pup census was made on 1st October. This figure was obtained on 2nd October.

TABLE 2

Censuses on Eilean nan Ron, 1957.

Date	Bulls, Cows, Juveniles	Passage	West Side	S. W. Side	Beaches	East Side	Totals	Total Adults	Total	Pups	Time of Census	Time of Daylight Low water	Height of Tide (feet and inches)	Springs and Neaps
4. ix	B	16	6	2	6	4	34				11.05		3. 9 ↓	(3. ix. 57 Neap)
	C	5	22	17	3	5	52	86 +3?	101	—	to	09.16		
	J	4	2	2	2	2	12				12.05		4.5 ↑	
5. ix	B	26	21	3	2	1	53				10.30		5.2 ↓	
	C	4	15	28	1	9	57	110	123	—	to	10.17		
	J	2	7	3	—	1	13				12.30		5.9 ↑	
6. ix											No Census			
7. ix	B	46	25	2	3	3	79				12.10		7.8 ↓	
	C	4	34	12	2	2	54	133	142	—	to	11.38		
	J	2	7	—	—	—	9				14.00		8.4 ↑	
8. ix	B	38	16	2	2	4	62				11.15–12.35		9.1 ↓	
	C	7	44	20	1	9	81	143 +2?	178	—	&	12.14		
	J	8	18	5	—	2	33				13.10–13.40		9.5 ↑	
9. ix	B	42	12	9	2	5	70				12.30–13.25		9.7 ↓	
	C	2	57	27	1	15	102	172 +2?	198	—	&	12.46		
	J	5	16	3	—	—	24				14.45–50		10.1 ↑	
10. ix	B	42	8	4	3	3	60				11.30		10.2 ↓	
	C	4	33	7	—	14	58	118 +2?	140	—	to	13.17		
	J	4	11	5	—	—	20				13.55		10.5 ↑	
11. ix	B	9	8	1	3	2	23				15. 45		10.2 ↓	
	C	—	20	8	2	6	36	59	69	1	to	13.45		Spring
	J	2	7	—	—	1	10				17.00		10.4 ↑	
12. ix	B	14	8	1	4	5	32				12.50		9.8 ↓	
	C	—	23	18	5	13	59	91 +1?	120	2	to	14.15		
	J	4	17	6	—	1	28				14.20		9.9 ↑	
13. ix	B	17	4*	3	4	2	30				13.15		9.0 ↓	
	C	6	13*	10	7	19	55	85* +27?	119	3	to	14.44		
	J	6	1*	—	—	—	7				15.30		9.0 ↑	
14. ix	B	11	3	1	6	4	25				15.00		8.0 ↓	
	C	7	16	7	7	26	63	88	100	4	to	15.20		
	J	3	3	6	—	—	12				15.55		7.9 ↑	

TABLE 2 *continued.*

Date	Bulls, Cows, Juveniles	Passage	West Side	S. W. Side	Beaches	East Side	Total	Total Adults	Total	Pups	Time of Census	Time of Daylight Low water	Height of Tide (feet and inches)	Springs and Neaps
15. ix											No Census			
16. ix	B	4	3	17	2	4	30				16.45		5.0 ↓	
	C	2	4	50	8	8	72	102	114	4	to	16.47		
	J	—	1	11	—	—	12				17.50		4.8 ↑	
17. ix											No Census			
18. ix	B	4	2	6	5	3	20				17.10	06.32	3.1 ↓	
	C	5	7	33	5	9	59	79 +1?	97	4	to			Neap
	J	3	3	11	—	—	17				17.50	19.49	3.7 ↑	
19. ix a.m.	B	7	1	2	4	6	20				10.15		3.5 ↓	
	C	4	3	32	12	10	61	81 +1?	94	6	to	08.55		
	J	3	—	9	—	—	12				11.20		4.6 ↑	
19. ix p.m.	B	1	1	10	4	2	18				19.10		3.5 ↓	
	C	—	6	29	11	5	51	69	80	7	to	—		
	J	—	—	11	—	—	11				19.55		4.6 ↑	
20. ix	B	4	1	10	6	4	25				10.30		5.3 ↓	
	C	4	—	30	13	7	54	79	97	9	to	10.03		
	J	2	1	15	—	—	18				11.50		6.7 ↑	
21. ix	B	5	1	4	5	2	17				11.00		7.1 ↓	
	C	1	3	18	17	5	44	61	72	11	to	10.49		
	J	1	—	10	—	—	11				12.20		8.7 ↑	
22. ix	B	—	1	6	3	1	11				13.40		9.0 ↓	
	C	—	1	13	18	1	33	44	48	14	to	11.29		
	J	—	—	4	—	—	4				14.20		10.5 ↑	
23. ix	B	1	—	2	5	—	8				11.45		10.5 ↓	
	C	—	2	15	13	3	33	41	42	16	to	12.08		
	J	1	—	—	—	—	1				12.20		11.8 ↑	
24. ix	B	—	—	—	4	2	6				10.40		11.6 ↓	
	C	—	—	3	13	5	21	27	28	16	to	12.46		
	J	—	—	1	—	—	1				11.30		12.6 ↑	
25. ix										17	No Census			Spring

* About 27 seals were disturbed by a visitor to the island on the West Side. Figures for bulls, cows and juveniles for West Side are therefore low, but the +27 ? are seals of undetermined sex on the West Side.

Other " undetermined sex " seals are indicated thus +2 ? in the column giving the total adults. Their exact location is unimportant in view of their low numbers.

around it, the neighbouring small skerries and Sgeir Leathan are all used for haul-out.

CENSUSES (Tables 1, 2, 3)

In 1956 comparatively few censuses were made. This was in part due to the shorter time available, made shorter still by absence from Eilean nan Ron from 27th–29th September, and also because in this first year the other observations which had to be made prevented any attempt at a daily census. Thus only three complete censuses were made of Eilean nan Ron and one of Eilean Ghaoidmeal and its neighbouring islands. Four counts were made of the pups on Eilean nan Ron.

In 1957, daily censuses were made on Eilean nan Ron in the period from 4th–24th September with the exception of three days, two due to bad visibility and the other because the seals were disturbed by visitors to the island. Censuses were made of Eilean Ghaoidmeal on 16th and 26th September, but, on account of bad weather, of none of the neighbouring islets.

Experience in 1956 showed that a census had to be made around low water, preferably just after, to obtain a maximum count. In all the counts the exact location of the seals was recorded using standard place names as far as possible. This has allowed later treatment of the figures as shown in Tables 1 and 2, of which the 1957 data clearly show movement of seals from one area to another or of their disappearance from an area.

TABLE 3

Census of Eilean nan Ron, 12th August, 1957.

	Bulls, Cows Unsexed Juveniles	Passages	West Side	S. W. Side	Beaches	East Side	Totals	Total Adults	Total	Time of Census	Time of Low Water
1st Census											
	Bulls	1	2	4	—	1	8				
	Cows	2	3	23	—	5	33			10·45	
	?	—	1	—	11	9	21	62	65	to	
	Juv.	—	1	1	—	1	3			12·15	
											13·26
2nd Census	Bulls	1	2	5	4	7	19				
	Cows	2	4	10	5	29	50			13·30	
	?	—	—	—	—	1	1	70	73	to	
	Juv.	—	1	1	—	1	3			15·30	
Observers		R.F.S.	R.F.S.	J.J.	J.D.	R.F.S. J.M.W. J.D.S.					

Records were also kept of the sexes, being described as bulls or cows of reasonable (though not necessarily absolute) maturity and juveniles, these latter being smaller animals which were not considered to be sexually active, and therefore not sexed.

In 1956 all counts were made by *both* of us and the sexual proportions as well as the total numbers agreed upon. In 1957, the larger collections were usually dealt with by both of us, but by that time we were much more confident of accurate sexing, having developed more satisfactory criteria than those used previously (Hewer & Backhouse, 1959).

The census made by the students on 12th August 1957 is probably accurate as regards totals : the figures for bulls is probably a minimum and that for cows a maximum since differentiation is not easy and young bulls can easily be mistaken for cows.

BEHAVIOUR OF THE COWS

The cow censuses of 1956 and 1957 present somewhat different pictures in detail, although the outlines are similar in the two years (Fig. 9 A & B).

In 1956 from 20th September to 1st October there is a steady rise in the number of cows associated with the pupping beaches (Table 1) : in actual counts, from ten to thirty-five and in numbers based upon pups eighteen to thirty-eight. Over the same period the number in the Passage dropped from twenty to four.

In 1957 observations were, of course, over an earlier period (Table 2). At no time from 4th September to 24th September were there many cows in the Passage, the number never exceeding seven (8th and 14th September) and on six occasions there were none. Three of these six days were 22nd, 23rd and 24th September. The slow but steady rise on the Beaches is visible, however, with eighteen on 22nd September, although there were only fourteen pups. The figure is, however, comparable with that of 1956.

The principal difference between the two years lies in the use of the western guts and the southern skerries as hauling out grounds instead of the Passage. From 4th to 14th September 1957, the first and second Guts West contained the higher number of cows. From 16th September onwards the S.W. side, comprising the skerries all along the south western end of the island, was well populated. A sudden rise in numbers in the second Gut East took place on 12th to 14th September, associated with strong northerly winds.

In general therefore it may be concluded that a larger number of full-term cows became attached to the island before the onset of pupping. Their particular points of haul-out appear to be dependent to some extent upon the prevailing wind.

As pupping begins more of the cows become attached to the breeding beaches. It also appears that many of the others depart at least temporarily, perhaps in the same way that has been recorded for Shillay (Hewer, 1957). On the other hand the marked drop in numbers on Eilean nan Ron in 1957 from 21st September may be due to the cows moving over to Eilean Ghaoidmeal for pupping (see pp. 172–3).

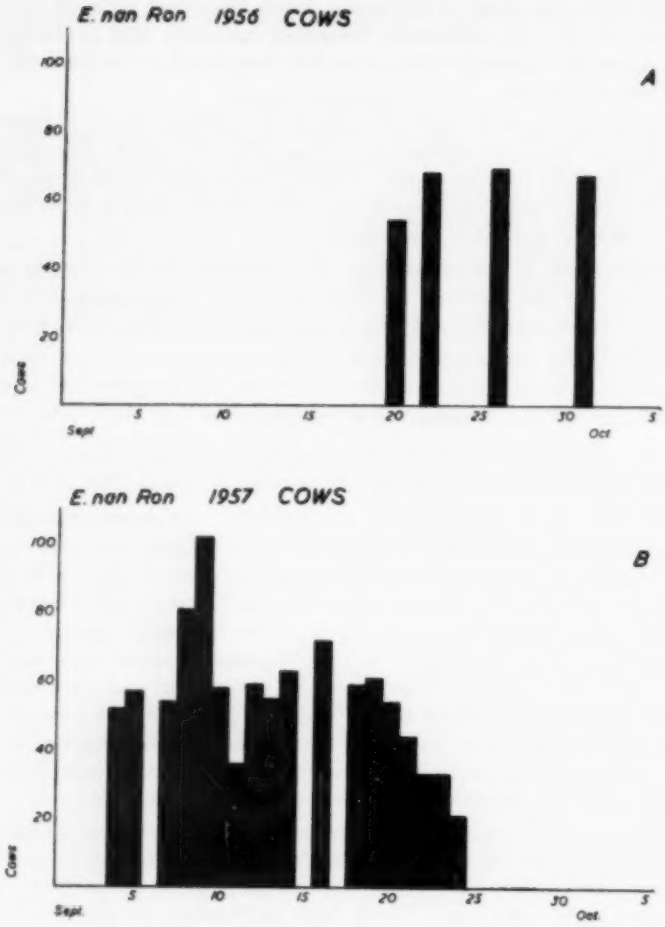


Fig. 9.—Histograms of numbers of cows present ; A—in 1956, B—in 1957. All based on actual counts.

The breeding beaches

Not all the beaches on Eilean nan Ron are used equally for breeding. The most populous are those at the south end, known as Beaches A, B and C (Fig. 4 and Pl. 2A). However, it was clear in 1956, from the age of pups found, that both first and second Guts East had been used very early on by one or two cows each of which had pupped on the shelving rocks well up these guts where they separated the three portions of the island.

Later several other beaches became used, South-west and West Beaches on the S.W. sections, Boat Beach and East Beaches North and South on the Central section and North Beach on the N.E. section. The most surprising

feature was the absence of any pups on Cottage Beach. This was a wide expanse of sand leading straight off first Gut East, well protected against all rough water and apparently perfectly suited as a breeding beach. It is, however, very close to the two kelpers' cottages, now roofless and for many years disused. Further it was noticeable that the N.E. section was very little used at all for haul-out or for pupping. This may possibly be because this section used to be inhabited for several months of the year by the kelpers and is the portion most frequently visited even now.

All the breeding beaches were connected to the sea, across the kelp area, by channels or guts. The convenience of these seems to be one of the principal factors determining their selection by the cows. Certainly Beaches A, B and C have the easiest approaches, with the exception of the few very small beaches off the Guts. This feature must be correlated with the habit of the cows of returning to the sea between periods of suckling, much in the way that they do in Pembrokeshire. Cows have been seen to make the journey to Beach B and to Beach A at least twice in a six hour period.

During these journeys the cows have to pass the bulls who have established territorial stations. The bulls nearly always approach the cows, obviously with the object of copulation. For about a fortnight the cows repel the bulls by hooting and flippering.

This antagonism appears to be a factor in keeping the bulls away from the breeding beaches. Nevertheless, under the stress of strong winds and a spring tide in 1956, some of the bulls were seen to come ashore on Beach A and to remain for at least three days among the cows and pups on a comparatively crowded beach.

In the visits made to Ghaoidmeal similar behaviour was noticed. In Fig. 8 the channels, which are comparatively few, are indicated and it was noted that the cows all made their way to the sea along them. All the available beaches were in use by the end of September in both years but the visit on 16th September 1957, showed that the early pupping had taken place principally on the South Sandy Beach and along the eastern beaches. However, by 26th September, the western beaches had many pups on them. Possible congestion on the beaches first used, or the easterly winds which had prevailed from 20th September may have been the cause. (Table 4).

In 1957 one cow pupped on 12th September on Beach B, the second to do so both on this beach and on Eilean nan Ron. The cow was totally blind. A hand causing a shadow could be passed across her eyes, yet she was able to suckle her pup regularly. Her disability also allowed her on one occasion to suckle the other pup on this beach and thereafter she accepted either pup. Her approach along the channel appeared to be by touch. She held in well to the side, brushing the kelp with her whiskers. However, when she turned along either Inner or Outer C channel (Fig. 6) she appeared to realise she was going in the wrong direction. After a few yards she would turn round, re-enter B Channel and resume her way towards Beach B. If disturbed when basking on the rocks at the side of the head of Beach B there was no hesitation in deciding how to re-enter the beach and in which direction to go. The only abnormality associated with this cow and pup was that the pup began to

moult when five days old and was completely moulted when only twelve days old. (Pl. 2 B). For a pup of that age it was well nourished and of reasonable dimensions.

TABLE 4

Weather Summary. Eilean nan Ron, September, 1957.

Date	Wind Force	Wind Direction	Precipitation	Date	Wind Force	Wind Direction	Precipitation
Sept.				Sept.			
3	L	←		15	M	→	showers
	S	→	nil		L	↘	nil
4	S	↖	rain	16	L	→	
	S	↗	nil		L	↗	drizzle
5	S	→		17	L	↖	drizzle
	S	→	showers		L	→	rain
6	S	↑	rain	18	L	↓	drizzle
	S	↗	showers		M	↓	nil
7	S	↗	nil	19	M	↓	nil
	M	→	showers		L	↓	showers
8	L	↘	showers	20	L	↙	
	M	↗	rain		L	↙	nil
9	L	↗		21	M	←	nil
	L	↗	showers		M	←	showers
10	S	↗	showers	22	S	←	rain
	L	↗	light showers		M	←	nil
11	M	→	light showers	23	M	←	
	S	↘	rain		M	←	nil
12	S	↘		24	S	↙	
	S	↓	storms		S	↙	nil
13	S	↓	showers	25	L	↙	
	S	↓	storms		L	↙	nil
14	S	↓		26	L	↘	
	M	↓	storms		L	↘	nil

L, light breeze ; M, moderate breeze ; S, strong breeze.

THE PUPS (Tables 5 and 6)

In 1956 a number of pups had been born before observations began. The onset of pupping had therefore to be estimated from the probable age of the oldest pups. For Eilean nan Ron this was based on observations on 22nd September when the oldest pup was estimated at sixteen days old, giving 6th September as a probable date for the onset (Fig. 1 A). Similar estimates were made for Eilean Ghaoidmeal on 22nd September (Fig. 10 B). These put the earliest pup as born on 2nd September. The proportion of early pups was higher on Eilean Ghaoidmeal than on Eilean nan Ron, thus confirming as probable an earlier date for the onset.

In 1957 the first pup was born on Eilean nan Ron on 11th September (Fig. 10 D & E). A visit to Eilean Ghaoidmeal was not possible until 16th September when some moulting pups were found. A probable date for the onset here was estimated as 31st August.

It will be shown later that the two groups of seals form parts of a single colony and that the date of the onset of pupping on Eilean nan Ron has little significance. That it was later in 1957 was probably due to the stormy weather experienced from 3rd to 11th September, and that it is always later than for Eilean Ghaoidmeal is due to the windward position of Eilean nan Ron. (Table 4).

Reports of early pups in the last week of August, born on the mainland of Colonsay confirm our observations that the onset of pupping may be stated in general terms as being at the end of August and the beginning of September.

The rate of pupping is at first low. Up to the middle of September it is probably about 1·0 to 1·5 a day. By 24th September it is probably about 7 to 8 a day. As no observations were made on Eilean Ghaoidmeal after 26th September (1957) it is not possible to give any idea of the highest rate, nor of the date of the peak, if indeed there be one. In fact, the evidence given by Mr J. Matthias (personal communication) that there were a number of pups and moulters well into November suggests that the total period of pupping may be prolonged well into October if not until the end of that month, with a pupping rate showing a flattened top from the middle of September until the middle of October. The number of pups counted and estimated from counts is shown in Fig. 10.

The lateness of the first pup on Eilean nan Ron in 1957 and the few pups counted there on 25th September compared with the numbers of 1956 suggested that the season of 1957 may have been a late one. The census of pups on Eilean Ghaoidmeal on 26th September, however, produced evidence which led to a very different conclusion. In Table 5 are set out counts for 23rd and 24th September, 1956 and for 25th and 26th September 1957. It will be seen that the total for 1956 is 105 and for 1957, 106. Taking into account that no pups were counted on Eileen Eoin and Cearn Rhioba in 1957 and that

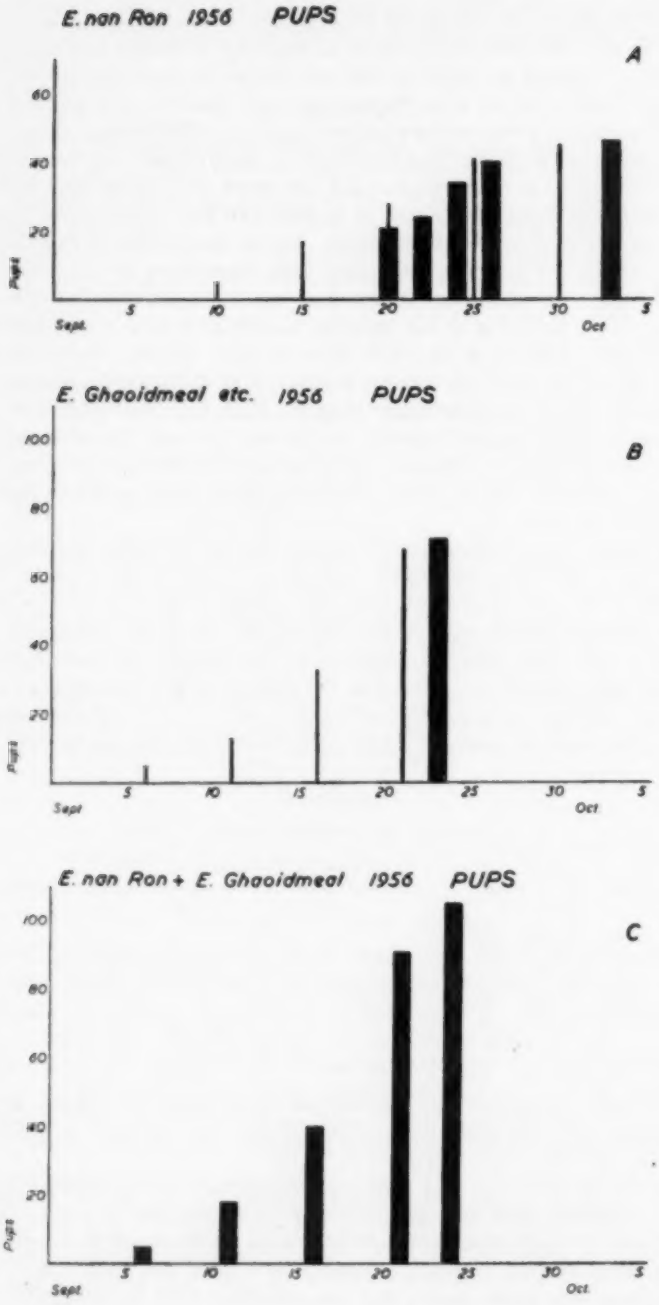
TABLE 5

Pupping—Comparable dates 1956 and 1957.

Year	Date	E. nan Ron	E. Ghaoidmeal	Total
1956	Sept. 23 24	34	71	105
1957	Sept. 25 26	17	89	106

the 1956 observations are two days earlier, these totals may almost be regarded as identical, and certainly comparable *if the breeding islands are considered collectively* (c.f. Fig. 10C & F).

Without observations of a numerical character during October it is impossible to calculate with any accuracy the total number of pups. Some idea of the order of magnitude of the colony may be obtained however by noting that by 25th to 26th September there are about 105 pups born ; that if a pupping rate of at least seven a day is maintained until the middle of October a


E. nan Ron 1956 PUPS
A
60
40
20
Pupæ
5
10
15
20
25
30
5
Sept.
Oct
E. Ghaoidmeal etc. 1956 PUPS
B
100
80
60
40
20
Pupæ
5
10
15
20
25
30
5
Sept
Oct
E. nan Ron + E. Ghaoidmeal 1956 PUPS
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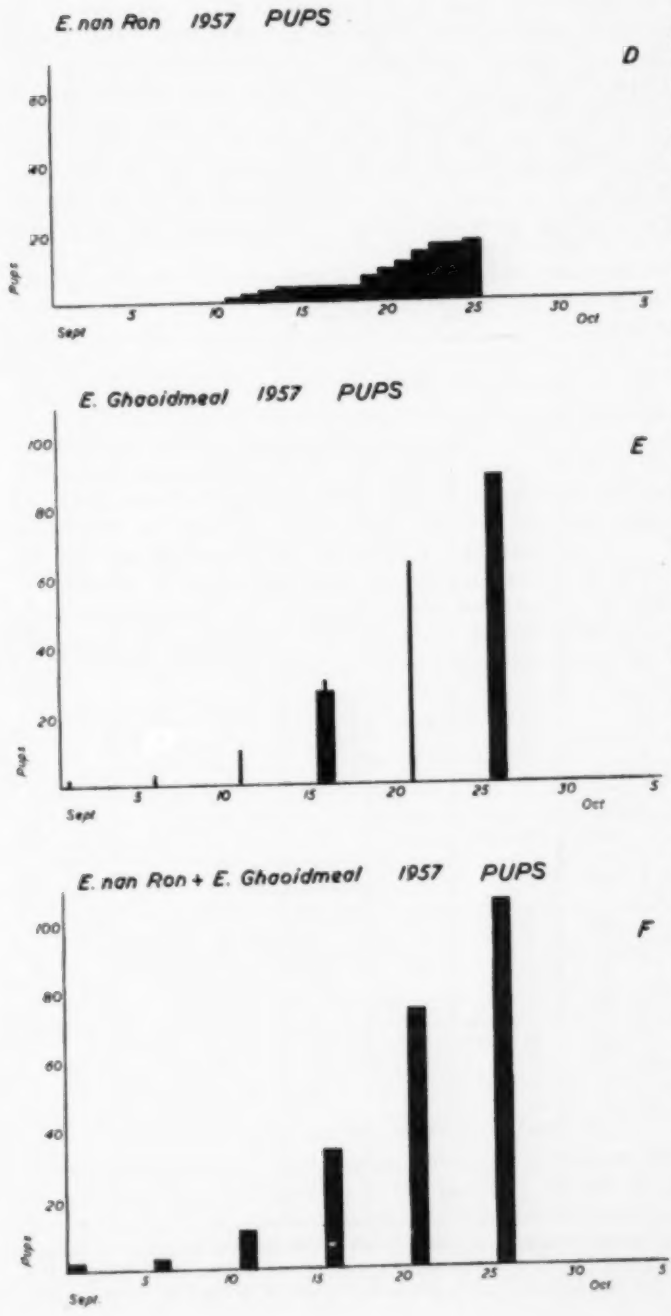


Fig. 10.—Histograms of number of pups ; A, B and C—in 1956 ; D, E and F—in 1957 ; A and D—on Eilean nan Ron ; B and E—on Eilean Ghaoidmeal and nearby skerries ; C and F—in the colony as a whole.
In A, B and E the narrow vertical lines represent estimated numbers based upon estimated ages of pups made on subsequent dates ; in A on 3rd October, in B on 23rd September, in E on 16th and 26th September.
In C and F the numbers are based upon both estimates and counts at five-day intervals.
In C the latest column is at a three-day interval and represents a minimum based on a count on E. Ghaoidmeal the day before. The second visit to E. Ghaoidmeal was prevented by bad weather.

further 140 pups will be born by then, to be followed by about 105 more as the pupping rate falls off at a rate similar to its rise in September. This would give a total of about 350 pups a year as a minimum, since the pupping rate may rise above seven a day and all the pups born up to 26th September had probably not been counted. The highest number of adult cows seen in any one day on Eilean nan Ron was 102 (11th September 1957) but on 22nd September 1956, about 90 were seen there and on the following day 99 were seen on Eilean Ghaoidmeal and the nearby islands making a total of 189. About half of these had not pupped (95 pups). It is not improbable that about half

TABLE 6

The Colony as a whole.

Eilean nan Ron			E. Ghaoidmeal etc.			Eilean nan Ron and E. Ghaoidmeal etc.		
Date	Bulls, Cows, Pups Juveniles	Nos.	Date	Bulls, Cows, Pups Juveniles	Nos.	Bulls, Cows, Pups Juveniles	Totals	Total Adults
16. 6. 57	B	30	16. 9. 57	B	25	B	55	174
	C	72		C	47	C	119	
	J	12		J	9	J	21	
	P	4		P	27	P	31	
22. 9. 56	B	44*	23. 9. 56	B	36	B	80	269
	C	90*		C	99	C	189	
	J	20		J	27	J	47	
	P	24		P	71	P	95	
24. 9. 57	B	6	26. 9. 57	B	10†	B	16	117
	C	21		C	80†	C	101	
	J	1		J	—†	J	1	
	P	16		P	89†	P	105	

* Partly estimated by apportionment of unsexed individuals (see Table 1).

† These figures apply only to E. Ghaoidmeal, the skerries not having been visited. The number of cows is less than the number of pups, so the number of adults is probably too low.

the potentially pupping cows had collected by that date around the breeding islands (see similar figures for Shillay in Hewer, 1956). These two approaches to the size of the pup population indicate a figure between 350 and 400 per annum.

The pups are born on the beaches and the majority remain there throughout their puppyhood and even sometime after moulting. A few tend to make excursions onto the kelp area when the tide is low. Some splash around in the rock pools on the beaches but not all beaches have such pools. At spring tides the beaches are covered by water and many of the pups are then forced to swim. Very occasionally pups are caught on the kelp area by the rising tide and swim about until they reach the beach. This has been observed in newly-born pups (less than twenty-four hours old) as well as in older ones. The purposeful entering of the sea by pups which is such a noticeable feature in Pembrokeshire is quite absent. So too is the movement of moulters away from their natal beaches which is also a constant phenomenon in Pembrokeshire.

Moulting for the most part appears to take place during the third and fourth weeks, when the pups are generally large and well fed. One exception however was noted and there may well have been others insufficiently recorded. This exception was the pup of the blind cow, who began moulting when five days old, completing it at twelve days. This pup was not under-nourished for its age and no adequate reason can be given for its early moult.

Data for the sex ratios are set out in Table 7, The totals for Eilean Ghaoidmeal are lower than the maxima possible in both years as twenty-eight pups in 1956 and thirty-three in 1957 were not sexed. The ratio falls within the limits already known (Hewer, 1957) and confirms a basic 1 : 1 ratio.

TABLE 7

Sex ratio of pups.

		Male	Female	Totals
1956	E. nan Ron	28	17	45
	E. Ghaoidmeal etc.	21	22	43
1957	E. nan Ron	7	10	17
	E. Ghaoidmeal etc.	31	25	56
	Totals	87	74	161
	Ratio	1·0	0·85	

THE BULLS ON EILEAN NAN RON

As pointed out previously by one of us (Hewer, 1957) the activities of the bulls during the establishment of the breeding colony are directed to quite another purpose than those of the cows. The establishment of dominance and then the acquisition of territory are the prime functions of the male activities. The cows are concerned at this stage only with finding a suitable beach on which to pup and to suckle the young.

From the census data (Tables 1 & 2 ; Fig. 11 A & B) it is clear that there is a great collection of bulls in the Passage in the early stages of colony build up. Those bulls scattered round the rest of the island are not attached to their positions. Observations made daily in 1957 showed that none of the bulls approached the breeding beaches until after the cows had pupped thereon.

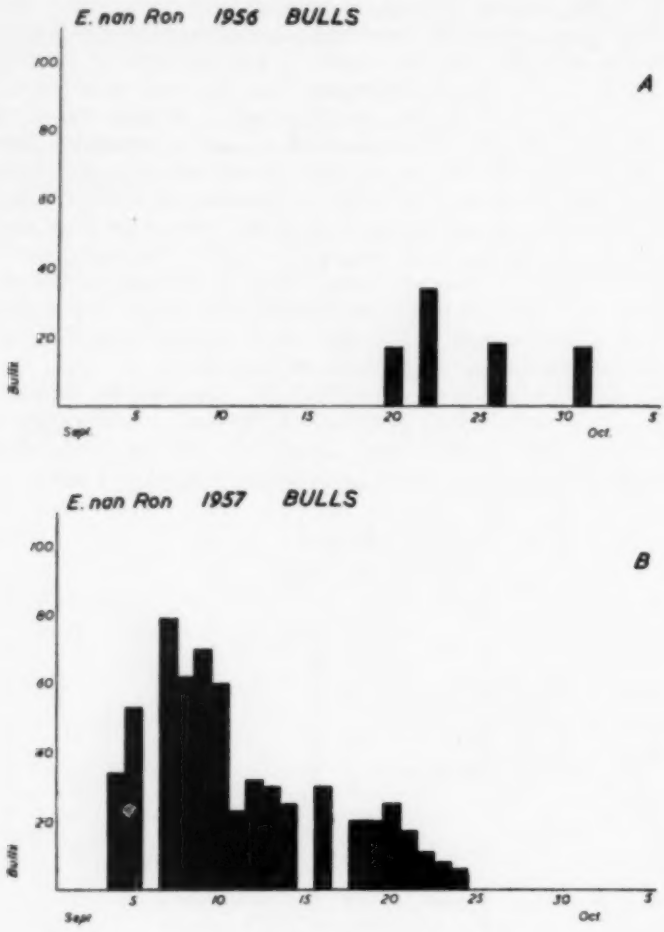


Fig. 11.—Histograms of numbers of bulls present ; A—in 1956, B—in 1957. All based on actual counts.

Despite repeated observations during the period of haul-out in daylight, no formal fighting among the bulls could be seen as a frequent or even normal activity. However, as the animals hauled-out there was usually some demonstration on the part of those already lying on the kelp against those attempting

to leave the water too close to them. This resulted in a considerable amount of hooting which could also be heard at night. Whether this is sufficient to establish priorities or not is not clear. It is possible that some antagonism may be displayed in the water but this was not observed.

In both 1956 and 1957 the principal haul-outs of bulls was towards the western end of the Passage, round the largest water area called " Bull Pool ". There were usually two or three large groups of ten to twenty bulls with one or two juveniles and a few isolated large bulls. The large groups contained bulls of a variety of ages, some very large. The segregation of some large bulls was a constant feature. The exact position of the groups varied from day to day. Lee positions were generally selected but this did not appear to account always for the precise choice. Frequently a seal would haul-out and soon be joined by others thus forming a nucleus which appeared to attract a larger number still. At other times those hauling out early would change positions so that the peak of haul-out would take place slightly later when more skerries were available, the earlier exposed skerries being by that time less easy of access by reason of steep walls. Factors such as these seemed, within the general plan of lee positions, to determine the precise locations from day to day.

Sketch maps (Fig. 12 A–D) show four consecutive days' haul-outs round " Bull Pool ".

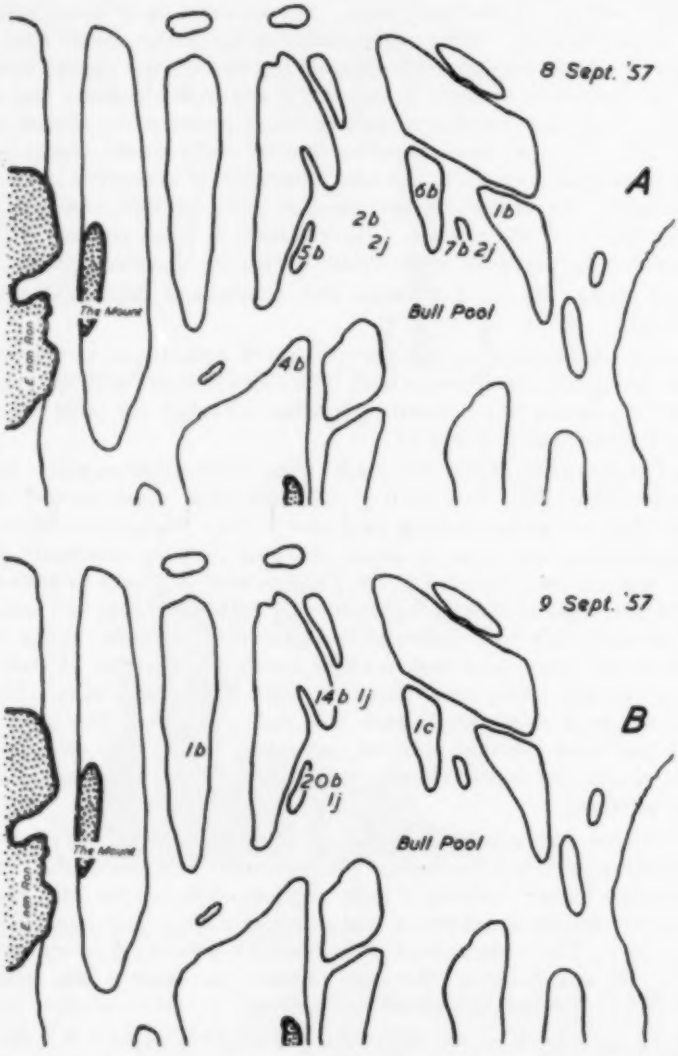
However, as the days passed the number of bulls began to decrease until very few remained in the Passage area. This synchronised with the appearance of more bulls nearer to the breeding beaches, although the total number also decreased considerably (Table 2).

Some comparisons must be made here between September 1956 and September 1957 (Fig. 11 A & B). Although both years showed this conspicuous drop in the number of bulls and in their disappearance principally from the Passage, the dates on which this took place are markedly different. In 1956 the numbers recorded in the Passage were still over fifty with a high percentage of bulls until 22nd September. By 26th September this had dropped to fifteen with only two bulls and to eight, with no bulls, by 1st October. Simultaneously there had been a slight rise in the number of bulls off the southern Beaches (22nd September—six, 26th September—ten). The departure of the seals from the Passage was rather abrupt. The noise of their hooting had been constant and very audible in camp. Its cessation on the evening of 24th September was remarked on and clearly indicated a sharp drop in their numbers.

In 1957 the most marked drop took place between 10th and 11th September (10th September—forty-two bulls, 11th September nine bulls) (Fig. 12 C & D) and although higher numbers of bulls were recorded on 12th–14th September, by 16th September the number had dropped to four and remained of that order or less. The decrease took place therefore a fortnight to ten days earlier in 1957. It was, however, the same phenomenon since it was accompanied by the similar increase in bulls off the Beaches.

Such a variation is quite considerable but might be explained on the grounds that the weather was exceptionally bad during the last fortnight of August,

and after a break of a few days, was followed by a further spell of storm from 3rd–16th September. Davies has recorded that the onset of stormy weather in Pembrokeshire tends to send the seals, particularly the bulls, onto the breeding coasts from the outlying skerries. Similarly on Eilean nan Ron, the stormy weather may have driven the seals in from the open sea to the comparative shelter of the islands at an unusually early date in 1957.



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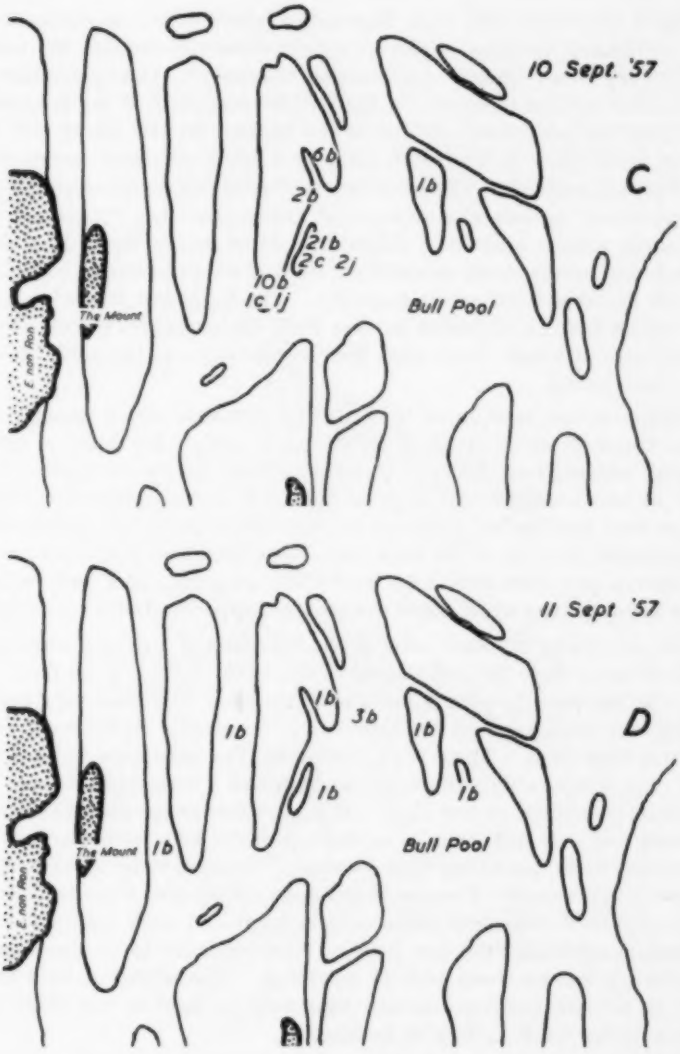

Fig. 12.—Sketch-map of skerries surrounding Bull Pool in the Passage, showing the numbers of bulls (b) cows (c) and juveniles (j) hauled out on the various skerries on four consecutive days in 1957. Note the different sites chosen on the different days and the sudden drop in numbers on 11th September. The totals on each of the four days were :—

8th	September—	bulls	25	cows	0	juveniles	4
9th	,,	—	,,	35	,,	1	,,	2
10th	,,	—	,,	40	,,	3	,,	3
11th	,,	—	,,	9	,,	0	,,	0

Territory

At about this time (9th–11th September 1957) bulls, generally of large size and obvious dominance, began to appear close inshore near the breeding beaches. They were clearly establishing territory. The procedure was exactly similar to that observed on Shillay (Hewer, 1957) if the kelp area be equated with the beach and wallows of the latter. At low tide a bull would be seen to come close in, and to remain in a particular spot for some time before returning seaward. The next day this would be repeated possibly with some exploratory movements around the point obviously considered by the bull to be the central point or " station ". After two or three days the bull would be found permanently established, driving off all intrusive bulls over an area which he considered as his territory. The bulls first to arrive took up stations which were undoubtedly the best from the point of view of the bull's future activity, although there were few, if any, signs at the time that these were the best places.

On Shillay it had been noted that the first two bulls which passed over the dunes to the wallows established territories in which the bulk of the cows would pup, although at the time of establishment of station there was only one cow in one territory and none in the other. Since however these two territories were the nearest to the shore they might have been selected solely on geographical grounds of convenience. On Eilean nan Ron the complexity of the terrain provided situations where the geographically inshore centres were not always those which gave the greatest opportunities for copulation.

Before describing in detail some of the instances of territory observed it is desirable to show that the positioning of the bulls offshore is, in fact, " territorial ". It has already been pointed out that the kelp area is very extensive, increasing the area exposed by four times for nearly eight hours between consecutive high tides. There is no doubt that the bulls regard this kelp area as land only temporarily submerged at high tide rather than as sea bottom temporarily uncovered at low tide. At high water neaps the bulls are really only awash and can just swim over the top of the kelp-covered rocks. This they continue to do, patrolling their territory. At high water springs, although there is a greater depth of water they again cruise over their territory until the tide ebbs and redeposits them on the kelp. At such high water it was quite customary during the last week in September for us to check each bull on station by known characteristic markings. The situation here therefore appears to be intermediate between that seen on land in the Hebrides and that seen in the water in Pembrokeshire.

Attention is now directed to Figs. 4–6 which show the complex situation on the southern end of Eilean nan Ron.

There are three main pupping beaches in this area, A, B, & C, each eventually having on them numbers of pups roughly proportional to their size. For example by 2nd October 1956 there were twenty-one pups on Beach A, four on Beach B and twelve on Beach C. These beaches can be approached from the sea along two groups of channels. Beach A has itself two channels, " A " East Channel and " A " South Channel, joining at " A " Pool ; it may also

be approached through the Lagoon and Lagoon Pool but the usual seaward entry into Lagoon is at the southern end of " A " South Channel so that this may be regarded merely as an alternative route. Beaches B and C have a single common approach from the east, " B " Channel. This channel, however, ends at " B " Pool close to the foot of Beach B. Just on the seaward side of this however there are two channels to the north, Inner and Outer " C " Channels leading to " C " Pool which lies at the foot of Beach C. These two channels enter " B " Channel at a widening known as Inner Pool. (Plate 1).

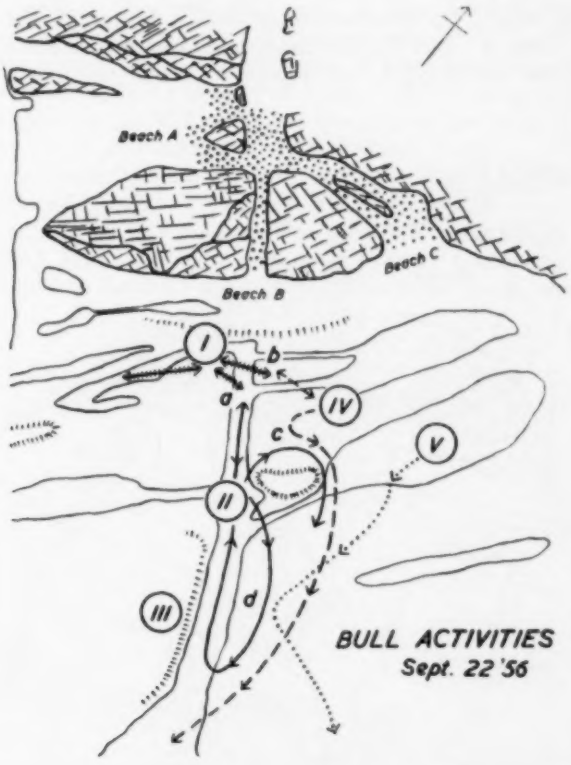

Fig. 13.—Sketch-map of the approaches to Beaches B and C on 22nd September 1956, showing the activities of bulls in defence and acquisition of territory. I, II, III, IV and V—normal position or " station " of bulls in their territory.

(*a*) contact between bulls I and II and repulse of bull I.

(*b*) contact between bulls I and IV and mutual retreat.

(*c*) contact between bulls I and IV, bull IV being repulsed and driven seaward, with bull I pursuing for a short distance.

(*d*) contact between bulls I and V, bull V being driven seaward, while bull I returns to station.

No account has yet been given in detail of the method by which bulls establish their territories. The procedure was only described in broad terms for Shillay (Hewer, 1956).

In 1956, by the time detailed observations on the behaviour of the bulls began, 22nd September, the early stages of territory formation had taken place. On that date, at the approaches to Beaches B and C two bulls had already established themselves and one of them (Bull II) actively engaged two other intrusive bulls and drove them away (Fig. 13). These two (Bulls IV and V) were sited to the north of B Channel and were unmolested when situated in the neighbourhood of C Pool. Bull II attacked them however when they attempted to enter B Channel. (Fig. 13 c & d). Beach B had two pups and Beach C, eight pups. On 24th September Bulls I, II and IV were again seen on station. (Plate 1). Bull III had disappeared and did not come back during our period of observation (up to 2nd October). A bull, possibly Bull V, was in

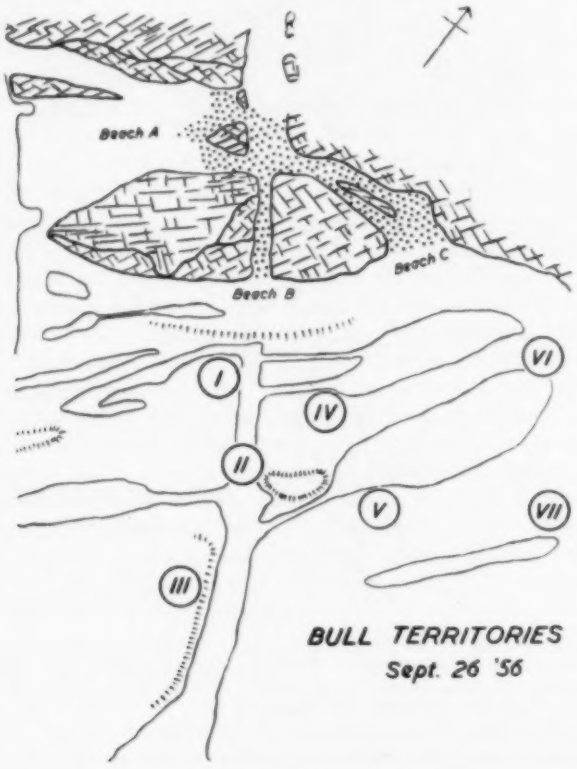

Fig. 14.—Sketch-map of the approaches to Beaches B and C on 26th September 1956, showing the stations occupied by bulls I–VII. Comparison with Fig. 13 shows that bull V has moved closer to bull I and bulls VI and VII have appeared on the eastern flank.

roughly the same position as that occupied by Bull V on 22nd September, but could not be positively identified.

A bull came from the sea to the position previously occupied by Bull III and began to move inshore. He was immediately attacked by Bull II and driven to sea. A further attempt by a bull to circle round Bull II to the south was also defeated when he found the inshore position occupied by Bull I.

Immediately after this Bull II copulated with a cow in B channel. During this copulation (the first seen in the colony), Bulls I and IV wandered well into the territory of Bull II without producing a reaction from Bull II.

On the approaches to Beach A three positions were occupied from 22nd September (1956) onwards (Fig. 15). These were Bulls A, B and C. Bull A was clearly dominant over the other two. A fight between Bulls A and C was witnessed on 21st September. There were eight pups on Beach A.

Observations were made on the night of 24th–25th September, at the midnight low water, from 00·15 to 00·55 hours. Bulls were seen at the normal positions occupied by Bulls A and C on the approaches to Beach A, and by Bulls I, II, IV and V on the approaches to Beaches B and C. Definite identification was impossible despite a full moon and a clear sky. Sexual activity was seen by Bulls II and IV but a clear copulation was not recorded.

On 26th September, the position was as follows :—Bulls A, B and C on station. Bulls I, II, IV and V on station but Bull IV had closed in a little on Bull II. In addition Bulls VI and VII appeared to the north-eastward of Bull V. (Fig. 14).

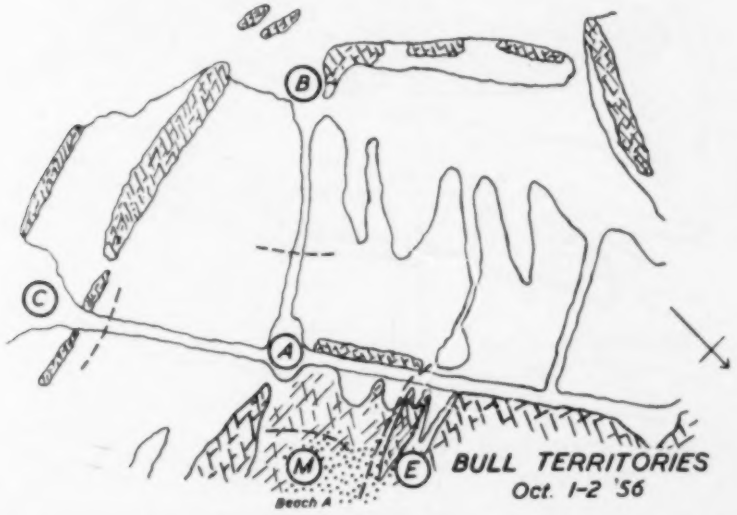

Fig. 15.—Sketch-map of the approaches to Beach A on 1st to 2nd October 1956, showing the the stations occupied by the bulls. Bulls A, B and C had been on station for about one week but bulls M and E had appeared only within the last two days. Their stations, although on the breeding beaches, are less favourable for the interception of the pupped cows than those of the three earlier established stations.

On 30th September, when observations were resumed, there was still a strong S.W. wind and, as the daylight high water (15.09 hours) approached, heavy seas were pounding the lower part of Beach A. The two bulls, one of which was Bull A, offshore in the water of A Pool and Lagoon, came ashore as the tide rose and the heavy breakers spread all across the kelp area. This was the first occasion that territorial bulls were seen on shore. Bull A hauled out in the centre of Beach A, the other (Bull M) at the western end.

On 1st October, three bulls were found on Beach A. The third one (Bull E) occupied a position inshore of Bull A which he may have reached from the east. Bull A was markedly dominant and still occupied the most favourable position, including A Pool. All three bulls displayed territorial behaviour. Other bulls had moved into the kelp area of the Lagoon but their behaviour was not noted in detail.

On 2nd October Bulls A, M and E still occupied their respective positions on the beach (Fig. 15). A census of pups showed the presence of twenty-two on Beach A, two on Beach B and thirteen on Beach C.

Bad weather prevented further observations in 1956. In 1957 observations covered the preceding period, from 4th–24th September. Up to 11th September the only appearances suggestive of the presence of territorial bulls

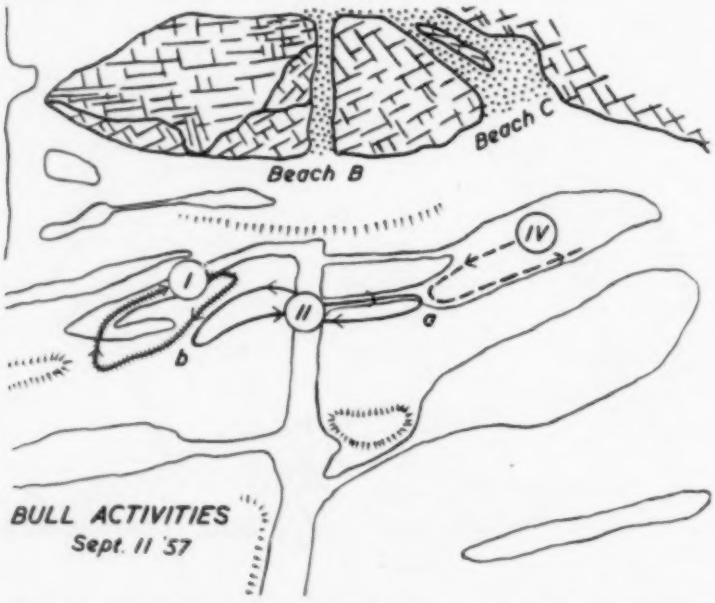

Fig. 16.—Sketch-map of the approaches to Beaches B and C on 11th September 1957 on which day the first pup to be born on E. nan Ron appeared on Beach B. Bulls I, II and IV are seen on similar stations to those of 1956 (c.f. Figs. 13 and 14). At (*a*) bull II repulsed bull IV and at (*b*) bull II repulsed bull I who moved seaward but returned to his station.

were the presence of large bulls in the " B " and " C " positions, at the seaward ends of A Channel South and A Channel East respectively. No pups had been born on any of the three beaches up to this date. Then, on 11th September, one was born on Beach B and a second on this beach appeared on 12th September.

On 11th September a large bull was found, in addition, installed in B Channel on the station of Bull II in 1956. The " C " position bull attempted to invade, possibly attracted by the cow (mother of the pup) but was beaten off with wounds. Another bull was present in C Channel and Pool (Bull IV position). Any attempts by Bull C (57) or Bull IV (57) to enter B Channel were defeated by vigorous responses by Bull II (57) (Fig. 16).

Since similar stations to those of 1956 were obviously about to be established a similar nomenclature was adopted, with the year attached. The intrusion by Bull C (57) on 11th September was the only observed mixing of individuals of the two sets of approaches. The development of the approaches to Beach A and to Beaches B and C will therefore be dealt with separately.

The approaches to Beaches B and C were the more advanced in territorial organisation, probably due to the presence from 12th September of two pups

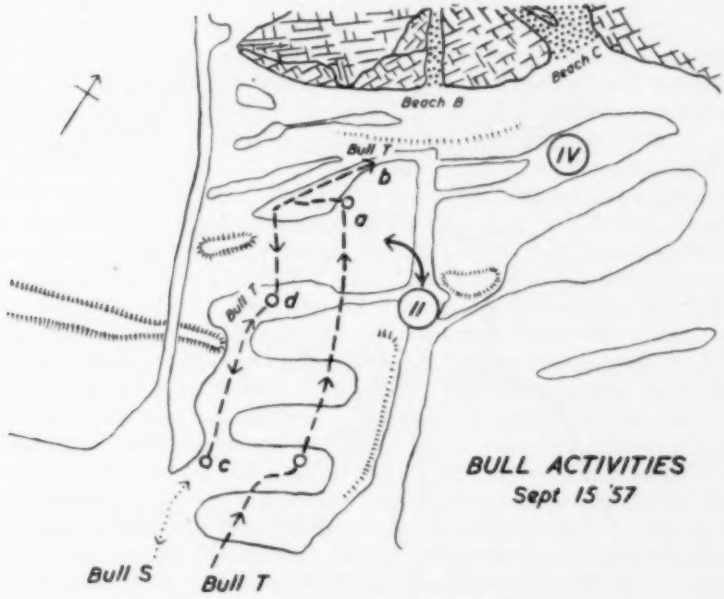

Fig. 17.—Sketch-map of the approaches to Beaches B and C on 15th September 1957. Bulls II and IV were on station. Bull T came over the kelp pausing where indicated by open circles. At (*a*) he was deflected southwestward by the approach of bull II but gains bull station at *b*. He then went out southward to the sea at *c* where he repulsed an intruding bull S who retreated. Bull T returned to *d*. It is not certain that bull T was identical with bull I, but compare with Fig. 18.

and their attendant cows. From this date onward Bull II (57) was constantly on station. Bull IV (57) was present in C Pool for 12th and 13th September but was not seen again until 17th September after which his attendance was fairly constant. On 12th, 14th and 15th September attempts to invade the area around B Channel were made. Bull II (57) was not always responsible for the retreat of the intruders. The record of 15th September is typical (Fig. 17).

> 14.05–14.35. Three intruder bulls attempted to move in from the sea as shown in diagram. Bull W did not come far. Bull T came into " Bull I " position but moved out again to repel Bull S who returned to sea, after an exchange of challenges. Bull II (57) being in water of B Channel (at lower level) did not see any of this.

Bull T remained until the end of observations on that day but no bull re-appeared to take up that station, so far as our observations went until 24th

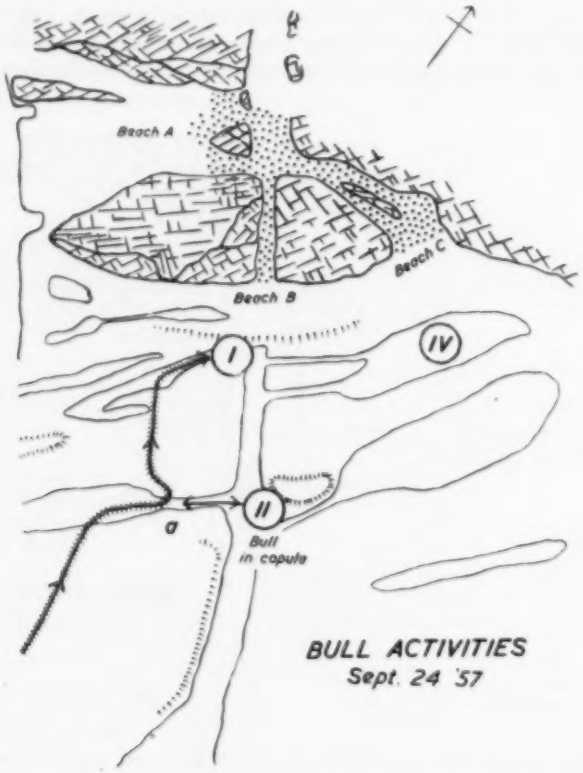

Fig. 18.—Sketch-map of the approaches to Beaches B and C on 24th September 1957. Bulls II and IV were on station. Bull II entered into copulation with the cow whose pup was born on 11th September. Bull I came in from the sea and achieved his station after being deflected at *a* by bull II.

September. He may have been later driven off by Bull II (57). Bulls II and IV remained in their stations throughout 17th–21st September without much interference from intruders. Bull II was the dominant bull and kept Bull IV well within C Pool. His territory was now shown to be very extensive spreading over the area from C Pool to A Channel East and from the shore to Outer Pool along B Channel. No observations were made on 22nd and 23rd September but on 24th September a bull came in and established himself in Bull I position with only a show of opposition by Bull II, who had just made his first copulation in B Channel with the mother of the first pup on Beach B. (Fig. 18). The situation with Bulls I, II and IV on station was now almost identical with that observed on 24th September, 1956.

In the approaches to Beach A it was not until 13th September that any large bull appeared inshore. On that day a bull was seen in A Channel East and in A Pool and Cross Channel. He remained for only a very short time before returning southward to sea. There was also Bull C (57) on station and a large bull in Lagoon. From 14th–18th September the position remained unchanged with Bull C (57) in station almost constantly and with a bull in " B " position more irregularly. On 18th September a cow was seen in A Pool and Cross Channel whither Bull C (57) had pursued her.

On 19th September there was a pup on Beach A. Its mother was in almost constant attendance on the beach or in the inshore approaches. Two other cows appeared from time to time either on the beach or in the Lagoon. Simultaneously Bull A (57) took up station in A Pool and another bull entered the Lagoon (Bull L). By the end of the day there was some definition of territory between the two at the junction of Cross Channel and Lagoon Pool.

On 20th September Bull A (57) was absent until 12.45 when he came into A Pool via A Channel South. Bull L was present in Lagoon and Lagoon Pool, but was driven off southward to sea after the arrival of Bull A (57). Another bull was present for some time during the morning at " B " position but disappeared before the arrival of Bull A (57). Bull L returned later and remained in " B " position. Bull C (57) was on station throughout the day. There were a number of cows in Lagoon and in A Channels South and East.

The following day opened with Bull L in " B " position and no bull in A Pool (Fig. 19A). Between 12.43 and 12.56 hours a bull came in over Rock Ridge to A Channel East and into A Pool. This was a smallish bull *not* Bull A(57) as subsequent events proved. Between 12.49 and 13.12 two attempts were made by a bull (later seen to be Bull A (57)) to enter the Lagoon over the Inner Southern Skerries but he was driven out again by Bull L (Fig. 19 A). A third attempt at 13.18 (Fig. 19 B) was successful as Bull L was at that time in the western part of Lagoon. Bull A (57) entered A Channel South and as he approached A Pool, the smallish bull there left hurriedly by A Channel East without staying to fight. He was intercepted and attacked violently by Bull C (57) and the two were seen going out to sea as two strong bow waves. Bull A (57) entered A Pool and later in the day (Fig. 19 B) challenged Bull L as on 19th September at the junction of Cross Channel and Lagoon Pool.

Thus the situation was consolidated for Bulls A (57), C (57) and L. No observations were made on 22nd and 23rd September but on 24th September,

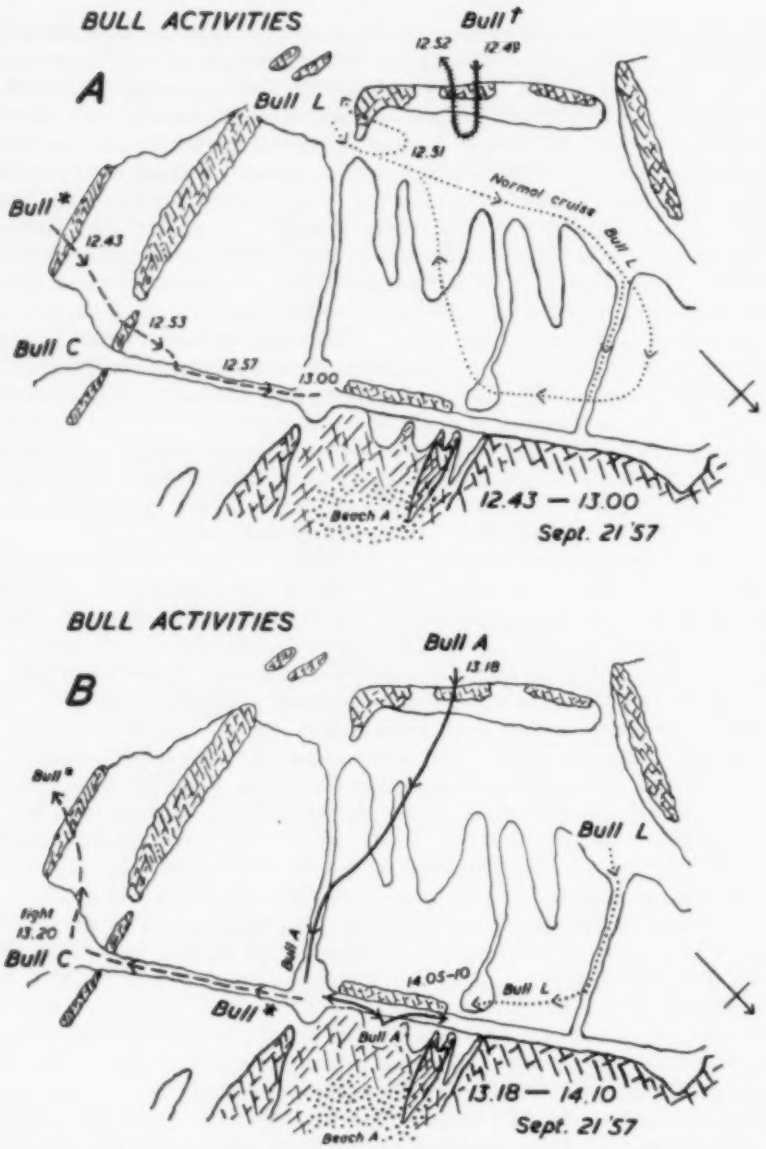

Fig. 19.—Sketch-maps of the approaches to Beach A on 21st September 1957.

A—12.43–13.00 hours ; an intruding bull* avoided bull C and arrived in A pool (bull A station), bull A being absent. Meanwhile bull † (probably to be identified with bull A) attempted to cross Lagoon but was intercepted at 12.51 by bull L who happened to be in that part of his normal course.

B—13.18–14.00 hours ; a little later bull A came in over the Lagoon while bull L was in the north-western part of his normal course. Bull* seeing bull A approach dashed down A Channel East where he was attacked by bull C and driven to sea. Later bull A and bull L exchanged challenges at Lagoon Pool.

the position was unchanged. With the exception of Bull L replacing Bull B (56) this corresponded with that of 22nd September 1956. It should be noted however that Bull D (56) seen at the western end of Beach A on 30th September 1956 may well have had territory in Lagoon during 27th–29th September when no observations were possible, and that Bull L as well as Bull A (57) might later come onto the beach. This latter conclusion is not certain since the appearance of bulls in Beach A in 1956 synchronised with a S.W. gale and spring tides. Bulls IV (56) and II (56) on the lee side did not come onto Beach B and Beach C respectively, although of course they may have done so after 2nd October 1956.

One feature is of particular interest. The taking up of territorial positions inshore synchronises with the first pupping, if it is not actually stimulated by the presence of the full-term cows. This was implicit in the establishment of wallow territories on Shillay but was not so clearly demonstrated.

Another feature of note was that the first stations to be established in 1957 were the most favourable ones in the light of *later developments*. Bull II (57) in the Inner Pool of B Channel was able to intercept cows from both Beach B and Beach C. Bull A (57) in A Pool was able to intercept cows moving to sea along either A Channels East or South and, by moving up Cross Channel (within his territory), those passing by Lagoon Pool into the larger Lagoon. The station of Bull I (57) is less favourable although it is closer inshore. Bull C (57) was in constant position somewhat earlier than Bull A(57), but the observation on 11th September showed that he had attempted to occupy the " II " position of the approaches to Beaches B and C and consequently might not be considered to be in competition for the approaches to Beach A until later. This view is borne out by a very peculiar observation on 19th September when Bull A (57) went down A East Channel, met Bull C (57) and *returned together without fighting*, Bull A (57) going into A Pool while Bull C (57) went back to station.*

The general picture which is therefore presented of the bull territories and stations, resembles that seen on Shillay and on North Rona (Darling, 1939) namely a chequer-board of territories. Those first established are large and centred on the most favourable positions *for the interception of pupped cows.* It is here that the organisation of the colony on Eilean nan Ron differs so markedly from the Hebridean. On Eilean nan Ron the bulls at first are seaward of the beaches, not on the beaches nor on the landward pupping grounds. Their territorial " land " is unsuitable for pupping but eminently suitable for interception, the behaviour of the cows in returning to the sea from the beaches on which their pups lie providing the opportunities. It should here be noted that although the cows in Pembrokeshire also return to the sea between periods of suckling, the bulls lie still farther seaward so that interception cannot occur. On Shillay the cows which pup on the beach also go into the sea but the bulls rarely intercept because they are stationed on the pupping beaches themselves.

Comparison with conditions in the Treshnish Islands is interesting. Darling

* This observation was made by both of us to our complete astonishment. The possible explanation only occurred to us later.

has described a similar lowered beach but of inconsiderable width surrounding the islands. Here the bulls are arranged in a linear fashion along the shore on which the pupping takes place ; there literally is no room for the chequer-board pattern of territories. Otherwise the position is similar to that on Eilean nan Ron, the bulls intercepting the cows.

Continuous observation on Eilean Ghaoidmeal has not so far been possible. However, such observations as were made showed that in those parts where the kelp area was extensive the position could be similar to Eilean nan Ron. At the southern end a second bull was seen seaward of the main bull attached to the Southern Sandy Beach. On the west coast, however, in the vicinity of the dyke, the kelp is narrow and only one bull was seen between the beach and the shore. Here then the position is similar to that in the Treshnish Islands.

Territorial Fighting. In general the defence of territory followed the usual procedure observed on Shillay. As soon as the owner bull saw an intruder, he made towards him, pausing on the way to challenge, with lowered head and open mouth. Usually the intruder would turn round and retreat to sea, but some, more persistent, would merely sheer off and attempt to obtain the desired position by skirting round the occupied territory. This might succeed but particularly active defenders would continue the chase until the defeat of the intruder either by withdrawal or by suffering damage in actual combat.* To this extent the pattern was familiar. However, the victorious bull did not signalise his possession of territory by " rolling " as on Shillay. Only once did we observe a rather half-hearted roll and this appeared to be due as much to a sloping wet surface, covered in wet kelp, as to any active and purposeful " roll ". Many occasions were seen when, on Shillay, a roll would inevitably have followed, but did not on Eilean nan Ron.

MATING

Mating was observed on numerous occasions. On Eilean nan Ron, in 1956, it was first seen on 24th September and in 1957 also on 24th September. As observations on the preceding days in 1956 had not included long periods at the breeding beaches it is possible that a copulation had occurred before. The cow taking part on 24th September 1957, had given birth on 11th September. Both these copulations were in B Channel on Eilean nan Ron. In 1956 the oldest pups were found in the second Gut and there is little doubt that earlier matings take place both on Eilean nan Ron and on Eilean Ghaoidmeal involving the cows which pupped in the first week of September. In 1956 by the end of September copulations were of frequent occurrence.

Mating was always seen to take place in the channels. Activity in general was always at a minimum at both high and low water and copulations usually took place during ebb and flow when there was some water in the channels but the kelp area was not covered.

It has now been possible from daily observations to form a picture of the three stages of relationships between cows and bulls. During the earlier phase,

* Cine-film records of territorial acquisition and defence were made and included in a film " Eilean nan Ron ", a copy of which will be deposited with the Zoological Society of London.

when the bulls are still establishing and maintaining their maximum territory, cows, both those who have pupped and those still pregnant are approached by the territorial bulls. The cows repel the bulls with hooting and splashings sometimes actively attacking them. The bulls never fight back but withdraw sometimes snarling. This approach by the bull, *which is not pressed home*, may be a general reaction by the bull to any intrusive seal, cow or bull. If on closer contact the seal turns out to be a cow, the attacking reaction dies down and the bull retreats before the cow. This behaviour also has been observed on Shillay by one of us both among bulls newly landed and challenging, and among bulls established in the wallows and approaching actively all invading seals.

The second phase is characterised by the bull attacking the cow viciously and being equally violently repelled by her. The results are obvious in violent battles and splashings in the pools and channels. At this stage the bulls have established their territory and are less concerned with intruders from the outside than they are with the cows within their area. Moreover the number of cows is increasing and there is no doubt that the mere presence of cows tends to stimulate the bull's sexual activity. Few if any of the cows, however, are yet ready to mate and consequently the two animals are antagonistic. This phase has not been seen in Pembrokeshire nor was it obvious on Shillay. In the first there is not the proximity of the cows and bulls to stimulate them sufficiently, while in the second the energy expended by the bulls in establishing and maintaining their territory *on land* undoubtedly caused a severe drain on their physique. Certainly in the wallow area the earlier bulls showed a quiescent period until the cows were ready to receive them. The violence shown by the Oronsay bulls has also been reported as seen on the Farne Islands (Mrs Hickling *in verbis*), and on Lunga (O. Hook *in verbis*).

The third and final phase is that of true mating. Copulation takes place without undue splashing and struggling and was frequently seen by us only in routine scanning of the whole area : attention had not been attracted by any splashings.* The posture assumed is identical with that illustrated by one of us (Hewer, 1957) although only parts of the pair can be seen above water at any given moment. Quite often the pair sink below the surface for ten minutes or more. A normal period of copulation is about fifteen to twenty minutes, after which the two separate slowly, the bull usually returning to station and the cow moving down channel to the sea.

It is not yet possible to give any idea of the number of copulations which take place between a bull and a cow but it is undoubtedly more than twice. Nor is the number of cows serviced by one bull yet determined by direct observation.

SUMMARY

1. A breeding colony of grey seals is centred on Eilean Ghaoidmeal and Eilean nan Ron, south of Oronsay, Argyll. Breeding on a very limited scale also takes place on the neighbouring islets and a few pups are born on the

* O. Hook (in verbis) has recounted one successful mating, lasting nearly half an hour, which started by a display of violence. The cow may have been between phases two and three.

beaches of Colonsay. A very tentative figure of 350–400 pups each year is suggested for the whole colony.

2. Seventy or more seals (of both sexes) may haul out on Eilean nan Ron alone, in August.

3. The first birth is estimated at about 1st September and there were well over 100 pups (possibly 120–130) by the end of the month. No statistical evidence has yet been collected for October.

4. The breeding beaches are separated from the open sea by an erosion platform crossed by channels and covered only for about four hours at high water. After the pups are born the cows pass to and from the sea along the channels but occasionally cross the kelp-covered platform.

5. During mid-September a relatively large collection of bulls (40 +) hauls out on the skerries between Eilean nan Ron and Oronsay. All ages are present. There could not be observed any formal contests but the very large bulls tend to haul out separately as on Shillay. The numbers decreased rather suddenly, leaving only the older bulls.

6. With the onset of pupping on Eilean nan Ron, the remaining bulls established territory near the breeding beaches in chequer-board formation on the kelp-covered platform. The positions first chosen are those most favourable for the interception of cows along the channels.

7. The method of establishment and maintenance of territory by the bulls is described in detail.

8. The progressive change in the behaviour of the cows and bulls culminating in mating is described. Cows appear to be ready to mate about fourteen days after parturition.

9. In general the behaviour of both cows and bulls shows resemblances both to that seen in Pembrokeshire and, to a less extent, to that seen in the Hebrides. The presence of the erosion platform largely dictates the details of behaviour.

REFERENCES

Darling, F. F. (1939). *A naturalist on Rona*. Oxford.

Darling, F. F. (1947). *Natural history of the Highlands and Islands*. Pp. 222 *et seq.* London.

Davies, J. L. (1949). Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire. *Proc. zool. Soc. Lond.* **119** : 673–692.

Hewer, H. R. (1957). A Hebridean colony of grey seal *Halichoerus grypus* (Fab.). *Proc. zool. Soc. Lond.* **128** : 23–66.

Hewer, H. R. & Backhouse, K. M. (1959). Field identification of bulls and cows of the grey seal, *Halichoerus grypus* (Fab.). *Proc. zool. Soc. Lond.* **132** : 641–645.

EXPLANATION OF PLATES

Plate 1

Panorama over the approaches to Beaches B and C, taken from the rock between Beach B and Beach A (which lies behind the camera), 24th September 1956. The stations of bulls I–V are indicated and bulls I, II and IV are present, each to the left of the number. Five cows are hauled out within the territory of bull II to the left of B Channel. A cow is in B Pool close to bull I and her pup is clearly visible on the kelp towards Beach B.

Plate 2

A. Beach A, September 1956 at high-water. A typical breeding beach of the islands. The sides are rock bound but access to the land is easy at the head of the beach to the right

A colony of grey seals in the Southern Inner Hebrides.
Panorama over the approaches to Beach B and Beach C.

A

B

A colony of grey seals in the Southern Inner Hebrides.
A—Beach A at high-water. B—Two pups on Beach B.

of the picture. Heavy breakers can be seen at the seaward edge of the covered kelp area. Except at high-water the beach is completely protected. Only cows and pups are present on the beach.

B. Two pups on Beach B, 24th September 1957. The older pup is still unmoulted. The moulted pup is thirteen days old and a day younger and its mother totally blind. Both are obviously of comparable size and weight.

THE BREEDING BIOLOGY OF EQUATORIAL VERTEBRATES: REPRODUCTION OF THE LIZARD *AGAMA AGAMA LIONOTUS* BOULENGER AT LAT. 0° 01′ N.

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(With 2 figures in the text)

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INTRODUCTION

The Oxford University Expedition to the New Hebrides studied the breeding biology of the scink *Emoia cyanura* in the remarkably unvarying climate of Espiritu Santo at latitude 15° 15′ S. where it was found to reproduce the year round (Baker, 1947 a). There was, however, a breeding peak during November and December (during " summer ") and relatively few eggs were laid in May and June. The longest day in Santo is one hour forty-eight minutes longer than the shortest. The mean temperature of the hottest month is only about 2° C higher than that of the coolest and there is no dry season. In a subsequent publication (Baker, 1947 b) it was suggested that the breeding seasons of the New Hebridean vertebrates selected for study might be controlled by external factors not affecting the sense organs or meteorological instruments of Man.

The present contribution reports on a study of the terrestrial lizard *Agama agama* living almost on the equator near Nanyuki, East Africa (Fig. 1), where the longest day is only about two minutes longer than the shortest and where, therefore, there is no possibility of photoperiodic control of reproduction. Other aspects of the Nanyuki climate, which is more variable than that of Santo, are summarised briefly in Table I.

MATERIAL AND METHODS

When observed basking on rocks, the adult male was bright blue on the dorsal surface but, when captured, the blue area had changed to brownish-black. The lateral regions of the male are permanently rich terra cotta-orange, giving way caudally to a white-spotted area. White lateral caudal spikes are a prominent feature. Ventrally, the most conspicuous features are the paler terra cotta chest, black belly and prominent row of yellow genital scutes. The tail was missing (through former injury) in a large proportion of lizards and so it was impossible to consider total length (up to 13 inches) when determining a criterion for maturity. Males measured as much as 6 inches from snout to vent along the ventral surface.

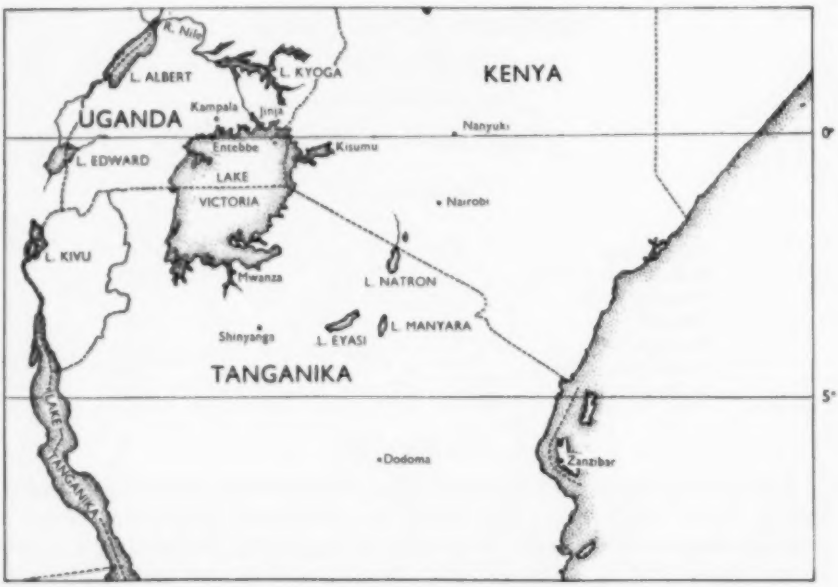

Fig. 1. Map showing the region of the present, and allied, studies.

The female lacks the brilliant blue and red, and its genital scutes are very pale yellow. Females grow to a length of 5¾ inches from vent to snout. Younger individuals of both sexes have longitudinal throat-stripes, alternating brown and white. Such stripes usually disappear when the snout-vent length is between 4 and 5¼ inches.

The present study is based on 103 adult male, 109 adult female and 36 juvenile lizards collected during the last days of every month of the year at Gadormurtu, situated at an altitude of some 5800 feet and about 3,500 metres south of the equator in the Kenya Highlands. Collecting activities were perforce spread over three years. *A. agama* feeds in open grass lands near

granite outcrops under which the animals take refuge when disturbed. They were captured for us by Africans who levered up the slabs, caught the lizards by hand and then killed them by concussion.

A series of fourteen males were dissected during the first month of collection (July, 1955) and it was found that all individuals measuring more than 4½ inches from snout to vent had wide tubule lumina containing at least some free spermatozoa. All reptiles with such a measurement of 4 inches also contained some spermatozoa, but the sexual development of those measuring about 3½ inches or less had not proceeded beyond mitotic spermatocytes. A snout-vent length of 4½ inches was therefore used as the criterion for the sexually adult male. Likewise, of seventeen females only those that attained the size of the sexually adult male were found to possess ovarian eggs containing yolk.

Subsequently, each monthly sample was preserved in formalin. After the first year's accumulation, dissections were completed by the removal of gonads and stomach contents. During the initial period, local difficulties made it impossible to collect in November, December and February so, a year later, supplementary collections were made from November to February inclusive. Monthly testis measurements are not given because the adult organ always measured between approximately 6 and 10 mm. in diameter.

OBSERVATIONS

July, 1955. The nine adult males contained massed spermatozoa with some free in the tubule lumina. All ten adult females contained large ovarian eggs, some of which were tinged with yolk. In three individuals there were shelled eggs in the oviduct. Breeding seemed to be near its peak. Stomachs contained principally black wing-cases of Coleoptera and remains of grasshoppers. The foliage present was probably wild clover leaves. Large leaf-shaped abdominal fat-bodies, anchored inguinally, were prominent.

August, 1955. Specimens (eight of each sex) were in a condition similar to those of July. The stomachs, too, contained the same proportion and kind of animal food. Fat-bodies were prominent.

September, 1955. The eight males were in the same condition as in July and August. Of twelve females, ten possessed slightly, and two had considerably, enlarged eggs but only one individual contained oviducal eggs. The breeding peak appeared to be past. Further, although Coleoptera and spiders were still present in stomachs, berries were now the principal food. Fat-bodies were still prominent.

October, 1955. Almost all the eight males contained massed spermatozoa but the tubules of some appeared to be almost spent, with only a few rows of spermatocytes remaining. All fourteen females possessed small yellowish ovarian eggs but none was in the oviduct. The breeding peak had passed. The diet was now predominantly grass, though the stomachs of a few individuals were packed with Coleoptera and some spiders.

January, 1956. Although all eight males contained spermatozoa none was free in the lumina which were now sometimes relatively narrow. The largest oocytes in the five females were a mere 3–4 mm. in diameter ; the animals appeared to be sexually quiescent. Food, however, remained plentiful.

Stomachs contained about equal proportions of animal and vegetable food. Whole ladybirds, and almost intact, inch-long green caterpillars had been ingested.

March, 1956. The tubules of the five males had spermatozoa free in their lumina. One testis showed traces of lipoidal metamorphosis around the sperm-heads. Of the seven females, three contained eggs measuring up to 7 mm. in diameter ; and the largest eggs were tinged with yolk. The males were obviously in full reproductive condition and the females appeared to be starting a new rhythm. The stomachs contained animal and vegetable material in about equal proportions.

April, 1956. All five males contained massed spermatozoa, but none was free in the lumina. The four females contained eggs not more advanced than in March ; there appeared to be a lull in development. Stomachs held mostly grass-seeds and foliage but some contained insects, including masses of reddish-black ants.

May, 1956. The three males all contained massed spermatozoa. The three females possessed ovarian eggs up to 6 mm. in diameter except one large female (5 4/5 inches from snout to vent) which contained eggs a mere 1·5 mm. in diameter. Sexual activity was clearly retarded. The diet was more or less equally proportioned vegetable and animal food, the latter being principally Coleoptera.

June, 1956. The five males were at the height of spermatogenesis, with the beginnings of tubule steatogenesis near the sperm-heads. The Leydig cells in some males were more heavily lipoidal than usual, giving the impression of a seasonal gain. Well-yolked eggs up to 7 mm. in diameter occurred in three females ; in the fourth, fully formed oviducal eggs were situated near the cloaca. Stomachs contained seeds and foliage, but caterpillars, Coleoptera and odd big Hymenoptera now predominated. The proportion of animal food has risen steeply and so had fat deposition in large leaf-shaped bodies. The seasonal sexual resurgence was now coming to fruition.

July, 1956. All five males contained massed spermatozoa, with some tubules showing a suggestion of steatogenesis near the sperm-heads. All seven females contained yolked eggs. The leaf-like fat bodies of all reptiles were heavier than before. Some females had as many as twelve big (9/10 × ½ inch) free eggs, displacing the liver and other viscera. Additionally, the ovaries, contained aggregations (measuring half an inch long) of yellowing ovarian eggs each about 4 mm. in diameter. Below these occurred another layer of colourless eggs each a fraction over 1 mm. in diameter. This remarkable succession of three stages of ripening or fully formed ova is doubtless an adaptation that enables rapid reproduction in times of plenty.

Compared with May, and even June, the ratio of animal to vegetable food had soared. The stomachs of many animals now contained only very small amounts of berries and grass : they were packed full of caterpillars and beetles. The visceral fat-bodies too, had enlarged enormously.

August, 1956. All eight males possessed massed spermatozoa of which many were free in the lumina. The six females all had yolked ovarian eggs. Some animals possessed distended oviducts and had obviously laid. One contained

nine shelled eggs together with yellow ovarian eggs and a generation of pale oocytes beneath them. Nevertheless, the principal food had become vegetable. Some lizards contained many yellow flowers not previously found in stomachs. Leaves were also eaten, as well as larvae, beetles and (once) the eggs of a smaller reptile.

November, 1956. All eight adult males contained massed spermatozoa but the seven mature females were sexually quiescent, possessing oocytes a mere 2 mm. in diameter. Oviducts remained distended from previous layings. Stomachs contained a greater proportion of vegetable food than animal, but every individual contained at least some insects.

December, 1956. The nine males and ten females were in the same condition as in November both in gonad condition and stomach contents. The oviducts remained distended.

January, 1957. The six males and six females were in the same condition as in November and December.

February, 1957. The eight males were in the condition of previous months except that spermatozoa were sometimes free in the lumina. The eight females fell into three categories. The ovarian eggs of five were small and lacked yolk. Those of two contained yolk and the remaining female additionally possessed shelled oviducal eggs. The proportions of ingested animal and vegetable food were about equal.

DISCUSSION

There is abundant evidence that the breeding seasons of birds are timed to coincide with the most prolific seasonal harvest of the food on which the young are fed (Shäfer, 1907 ; Davis, 1933 ; Marshall, 1942, 1950 ; Lack & Silva, 1949 ; Thomson, 1950).

At the same time, there has never been available absolute proof that it is the appearance of the food itself that operates as a timing device in any species. In most avian species it would seem that the external regulators are various. Certainly the sexual cycle in all birds so far investigated is seasonally reactivated months before the beginning of the annual food harvest ; although it is also probable that the females of at least some species (e.g. the Satin Bower-bird, *Ptilonorhynchus violaceus*) will ovulate only when adequate supplies of suitable food appear in the environment (Marshall, 1950).

In the lizard *Agama agama* reproduction does not appear to be influenced by rainfall *per se*. It does however coincide with the subsequent maximum occurrence of appropriate animal food. This was proved by analysis of stomach contents. Table I shows the important aspects of Nanyuki climate, and Fig. 2 further illustrates the distinct correlation between mean rainfall, the subsequent ingestion of increased quantities of animal food and, hand in hand with the heightened protein intake, seasonal egg-laying.

The variable Nanyuki rainfall occurs in the characteristic equatorial East African pattern of the so-called " long " and " short " rains that follow the passage of the sun overhead twice each year. These rains turn the upland

TABLE I

The Nanyuki Climate*

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean Rainfall											
0·43	1·43	1·82	4·06	2·90	1·96	1·90	3·07	2·17	2·64	2·83	1·53
Average No. of Days of Rain											
3	4	8	16	14	9	7	10	10	12	12	7
Mean Maximum Temperature											
77·5	78·5	77·3	75·0	73·6	74·1	71·9	72·6	75·3	74·4	72·7	73·6
Mean Minimum Temperature											
45·5	46·5	49·1	50·9	50·6	48·4	47·8	47·1	46·5	47·7	49·2	46·9
Mean Relative Humidity											
59	60	67	74	75	72	75	75	69	71	76	72

* Calculated over a period of six years.

veldt from brown to green and there is a corresponding upsurge of insect reproduction which allows many small avian species to breed twice a year although birds of most groups reproduce only during or after the " long rains " that fall from March to May.

The latter is apparently true of *Agama agama*. Our data show that from August to January vegetable food predominates in the stomachs and in February and March, after the " short rains ", the lizards found additional animal food. Nevertheless, only one female during this period was found to

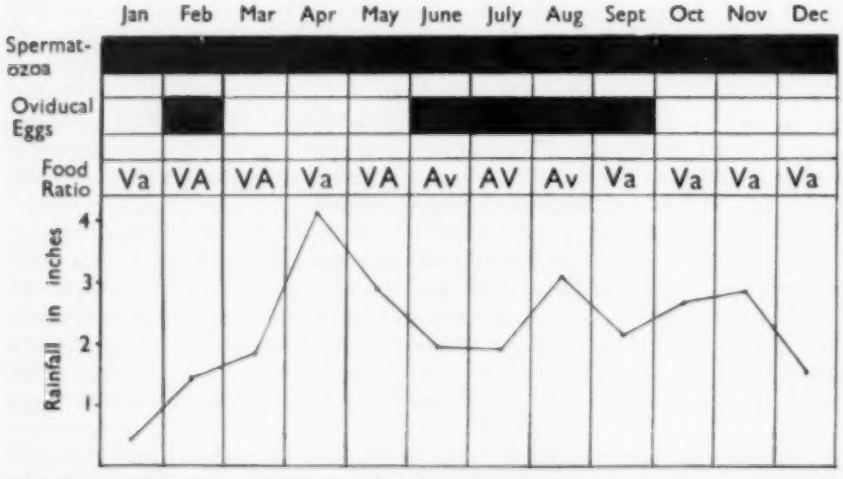

Fig. 2.—The sexual cycle of the equatorial *Agama agama lionotus* in relation to rainfall and to the proportion of ingested vegetable or animal food.

contain shelled eggs. The proportion of animal food fell away during April and ovulation did not occur even though this is the month with the heaviest rainfall. It was only after the effects of the " long rains " reflected in the increased protein intake of May to July inclusive, that the breeding season began (Fig. 2). During June and July relatively large, leaf-shaped fat bodies expanded in the abdominal cavity and stomachs were packed with caterpillars, beetles and Hymenoptera. In August the ratio of animal food dropped, and after September no more oviducal eggs were found.

The sexual cycles of male and female differ remarkably. No mature male was at any time of the year without bunched spermatozoa. No gross seasonal changes in testis dimensions such as occur in birds were detected. The organs of adults ranged always between 6 × 5 mm. and 10 × 8 mm. in size. In the British *Vipera berus* one spermatogenesis succeeds another after a very brief pause (Marshall & Woolf, 1956). The succeeding rhythm quickly produces spermatozoa but a halt is imposed during hibernation. In *A. agama* there appears to be an equally quick recovery of spermatogenetic function and, in the absence of hibernation, at least some activity appears to be continuous. Although in odd individuals the beginnings of steatogenesis were seen in the region of the bunched sperm-heads, no grossly lipoidal tubules (such as occur in some reptiles) were found. The males then, appear to be in a state of reproductive readiness whenever conditions become appropriate for reproduction.

There seems little doubt that the actual time of reproduction is dictated by external changes operating through the exteroceptors of the female. This is the normal pattern in birds (Marshall, 1951). Further, during the height of reproduction in July, some females contained developing or complete eggs in three distinct phases : 1, colourless ovarian eggs, surmounted by 2, a generation of yolked ovarian eggs and, free in the oviduct 3, as many as twelve shelled eggs ready to be laid. Here, it seems, is an adaptation whereby, upon the advent of optimum reproductive conditions, a single female can quickly thrust perhaps thirty or more eggs into the environment. Undoubtedly the cycle is timed to occur during the seasonal " flush " of highly proteinous insect food that is essential to the development of the young (Marshall, 1951). Furthermore, it appears likely that it is the seasonal increase of such food that is the specific stimulus to the female sexual cycle.

There remains the question why reproduction in this lizard is not more widespread in February and March when the proportion of ingested animal food arises after the so-called " short rains ".

Two obvious considerations arise. It may be that these rains are insufficient to provide conditions suitable for widespread reproduction or, on the other hand, that breeding is inhibited by the relatively low night temperatures that prevail between December and March. We incline to the latter view. It is possibly not without significance, however, that examination of local weather records showed that the exceptional sexual activity noted in February 1957 occurred after an unusually heavy rainfall of 3·12 inches during the previous December. The following January and February were almost without rain.

SUMMARY

1. The equatorial lizard *Agama agama lionotus* possesses a distinct breeding period which occurs during the peak of the seasonal harvest of protein animal food that follows the so-called " long rains ". The males contain bunches of spermatozoa throughout the year.

2. As the proportion of ingested animal food increases, the sexual condition of the females heightens. There is a concurrent growth of large leaf-shaped abdominal fat bodies. Widespread egg-laying occurs during four months of the year (June–September inclusive), the peak being in July and early in August.

3. During the height of reproduction three distinct phases of egg development can be seen macroscopically : 1, a layer of colourless ovarian eggs surmounted by 2, a series of yolked eggs and 3, a clutch of ten to twelve shelled oviducal eggs. This device enables quick and repeated ovulation during the period of the maximum insect harvest.

4. During the period of study one ovulation only was recorded after the so-called " short rains ". This occurred in February and after unusually heavy precipitation during the previous December.

5. Any possibility of the photoperiodic control of reproduction was eliminated by the choice of the collecting locality. It is suggested that the sexual cycle of *Agama agama* is timed not by rainfall but by the seasonal appearance of proteinous insect food. Vegetable food of various kinds seems to be relatively abundant throughout the year. It is not known whether widespread reproduction after the secondary " short rains " is inhibited by a relative lack of protein food or, perhaps more probably, by the comparatively low night temperatures that occur from December to February inclusive.

6. *A. agama* is almost omnivorous, feeding on grass, berries, seeds, flowers, caterpillars, beetles, spiders, ants, Hymenoptera and the eggs of smaller reptiles.

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REFERENCES

Baker, J. R. (1947 a). The seasons in a tropical rain-forest, 6. Lizard (*Emoia*). *J. Linn. Soc.* (Zool.) **41** : 243.

Baker, J. R. (1947 b). The seasons in a tropical rain-forest. 7. Summary and general conclusions. *J. Linn. Soc.* (Zool.) **41** : 248.

Davis, W. B. (1933). The span of the nesting season of birds in Butte country, California, in relation to their food. *Condor* **35** : 151.

Lack, D. & Silva, E. T. (1949). The weight of nestling robins. *Ibis* **91** : 64.

MARSHALL, A. J. (1942). *Display and bower-building in bower-birds.* Thesis : University of Sydney.

MARSHALL, A. J. (1950). The function of the bower of the satin bower-bird in the light of experimental modification of the breeding cycle. *Nature, Lond.* **165** : 388.

MARSHALL, A. J. (1951). Food availability as a timing factor in the sexual cycle of birds. *Emu* **50** : 267.

MARSHALL, A. J. & WOOLF, F. M. (1957). Seasonal lipid changes in the sexual elements of a male snake, *Vipera berus*. *Quart. J. micr. Sci.* **98** : 89.

SCHÄFER, E. A. (1907). On the incidence of daylight as a determining factor in bird migration. *Nature, Lond.* **77** : 159.

THOMSON, A. L. (1950). Factors determining the breeding seasons of birds : an introductory review. *Ibis* **92** : 173.

REMARKS ON THE STOMACH AND THE SYSTEMATIC POSITION OF THE TYLOPODA

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(With 3 plates)

The differences in the anatomy of the stomachs of the Tylopoda and the typical Ruminantia are shown. To be mentioned especially are the glandular sacs of tylopods and the differences in structure of the oesophageal groove. It seems likely that the Tylopoda and the Ruminantia have acquired the faculty of ruminating independently one from the other. The similarity of the stomachs is interpreted as a result of parallel-development and not as a result of a close relationship of the two groups. In the system of Artiodactyla the Tylopoda should be distinguished from the Ruminantia.

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INTRODUCTION

Within the order Artiodactyla Owen, 1848, there are two groups of ruminating animals, which, because of this physiological common factor, were often classed together in classical taxonomy as Ruminantia, and were contrasted with the non-ruminating cloven-hoofed animals (e.g. Gregory, 1910 ; Hilzheimer, 1916 ; Weber, 1928 ; recently also Romer, 1945, and Grassé, 1955). These are, on the one hand, the Tylopoda Illiger, 1811, and on the other, the Pecora L., 1758, and the Tragulina Flower, 1883. Modern taxonomists on the other hand confine the name Ruminantia Scopoli, 1777, to the Pecora and Tragulina, and give the Tylopoda a special place of its own. Simpson (1945) classifies the recent Artiodactyla, primarily on grounds of palaeontological evidence, within the suborders Suiformes, Tylopoda and Ruminantia. Lavocat (1958) also supports the palaeontologist's point of view that the Tylopoda are to be distinguished from the Ruminantia in the narrower sense. In the discussion following Lavocat's lecture in the Paris Colloquium in 1957, both Frechkop (1958) and Anthony (1958) particularly opposed this viewpoint, emphasizing that the Tylopoda do in fact ruminate too, and should not be distinguished from the other Ruminantia. The important question is, whether, with the Tylopoda, there is a deviation from the type of normal ruminant, or whether they present us with a special form. Expressed in another way, the question is :—has the capacity to ruminate been developed in the course of phylogeny of the Artiodactyla only once, or quite independently, twice? Since the

stomach is physiologically most closely connected with ruminating, a study of the stomach anatomy of the Tylopoda is of primary importance for the clarification of this question.

In the older anatomical literature, the parts of the stomach of the Tylopoda are homologized with those of the Ruminantia. According to Boas (1890) this is the case except for the reticulum. Boas considers the tylopod stomach to be more primitive than that of the Ruminantia and he tries to explain the peculiarities of the stomach of the Tylopoda from this standpoint. The most striking feature of the camelid stomach is the existence of the " sacs " in the rumen and reticulum. These structures are known in the literature as water-cells, to which a water-storage function has been long ascribed. This opinion has been given in many text-books right up to recent times (Hilzheimer, 1913, 1916 ; Schimkewitsch, 1921 ; Young, 1950; Colbert, 1955 ; Frechkop, 1955). During their South-America Expedition (1956–57), Herre and Röhrs observed during the dissection of South-American tylopods, that there was no water in these water-cells but a food substance in about the same, or even more solid condition as the content of the rumen. Stimulated by these observations, we have followed up in the material of this South-America Expedition, the problems which the stomach of the Tylopoda presents (Bohlken & Neteler, in preparation. The examination of the literature confirmed that our views on the function of the stomach-wall sacs must be revised.

In 1956 and 1957 a series of works were published which dealt with the water-metabolism of the camel and with the anatomy of its stomach. By means of physiological methods it was proved that the so-called water-cells do not have a water-storage function (Schmidt-Nielsen, Schmidt-Nielsen, Houpt & Jarnum, 1956). Petter (1956) gave a survey of the history of this misconception and its elucidation. Finally, Hansen & Schmidt-Nielsen (1957) described the anatomy and histology of the camel's stomach. These authors confirmed anew, that the stomach pockets are covered with glandular epithelium, a fact which Boas (1890) and others before him had ascertained. They therefore proposed to use the term glandular sac areas (Areae glandulosae sacculatae) for the stomach wall sacs. The mucous membrane of the omasum of the Tylopoda also contains glands. These glands are, just as in the glandular sacs, of a similar structure to cardiac glands. Fundus and pyloric glands are found only in the abomasum. Hansen & Schmidt-Nielsen (1957) were able to further show, that the glandular sacs are provided with a muscular structure which, in conjunction with the remaining stomach wall muscles, permits intake and disposal of the stomach content. These glandular sac muscles are however in no way sphincter muscles, as they were often taken to be earlier, and they do not accomplish a closing off of the sacs from the cavity comprising the remaining part of the stomach. These authors also discuss the possible functional importance of the glandular sacs, without however arriving at a final conclusion.

MATERIAL

For the investigation of the stomach of the New-World Tylopoda the main material available was of the Herre/Röhrs South-America Expedition (1956–57),

this consisted of one stomach of an adult guanaco, two complete foetuses of llama and four foetal stomachs of vicuna. Besides this material another stomach of an adult guanaco and one of an adult llama taken from animals dissected in the zoological gardens of C. Hagenbeck in Hamburg were at our disposal. For comparison, a stomach of an adult domestic sheep and some foetal stomachs of domestic ox were examined.

COMPARISON OF THE STOMACHS OF TYLOPODA AND RUMINANTIA

In order to come nearer to a solution of the question posed, the taxonomical value of the physiological characteristic known as ruminating, it appears useful to compare the stomach of the Tylopoda directly with that of typical Ruminantia.

1. *Exterior*

The stomach of Ruminantia consists of four parts, viz., rumen, reticulum, omasum and abomasum, the first three of which are called proventriculi. Like Hansen& Schmidt-Nielsen (1957) we follow the usual custom and use the same terms for the stomach compartments of the Tylopoda until the question as to the homology of the stomach divisions of Tylopoda and of Ruminantia is conclusively decided. The arrangement of the stomach compartments in Tylopoda and in Ruminantia is shown schematically in Pl. 1, fig. 1. This diagram makes clear some important differences between the Tylopoda and the Ruminantia:—with the Ruminantia the oesophagus joins the stomach at a point between rumen and reticulum; with the Tylopoda, on the other hand, the oesophagus discharges only into the rumen. In the rumen of the Tylopoda there are no pillars and, except for the glandular sac areas, the rumen is externally smooth (Pl. 1, fig. 2), whereas in the rumen of the Ruminantia there are strong muscular pillars (Pilae ruminis). Externally these pillars are visible on the rumen as grooves (Pl. 1, fig. 3). Even from the diagram (Pl. 1, fig. 1) it may be seen, that there are great differences between Ruminantia and Tylopoda in the shape of omasum and abomasum. The omasum of the Ruminantia is kidney-shaped and sharply separated from the reticulum at the one side and the abomasum at the other side (Pl. 1, fig. 3). With the Tylopoda the omasum and the abomasum form together a long section, in which from outside no delimitation between these compartments is to be seen (Pl. 1, fig. 2). However, the condition of the mucous membrane makes a division possible, as will be shown below.

The most remarkable peculiarity of the tylopod stomach, which has given rise to much discussion, are the glandular sac areas in the rumen and the reticulum (water-cells) (Pl. 1, fig. 4). There are two such areas in the rumen, the larger of which continues into the glandular sac area of the reticulum. These glandular sacs characterize the tylopod stomach and distinguish it from that of the Ruminantia.

2. *Interior*

Oesophageal groove. The comparison of the condition of the inner surfaces of the stomachs in both groups at first shows a difference in the outer structure of the oesophageal groove (Sulcus reticuli). In the Ruminantia the oesopha-

geal groove is marked off by two strong lips or edges, which begin at the cardia and pass on the wall of the rumen and reticulum to the reticulo-omasal orifice (Pl. 1, figs. 5 and 6). The length of the oesophageal groove from the oesophagus to the opening into the omasum is short in the Ruminantia. In the Tylopoda the oesophageal groove is single-lipped, and the distance between the point of entry of the oesophagus and the reticulo-omasal opening is very much greater. (Pl. 1, fig. 7). This difference in the length of the oesophageal groove makes clear again the differing position of the oesophagus opening in Ruminantia and in Tylopoda. Boas (1890) and Pernkopf & Lehner (1937) maintain that in the camel there are two oesophageal groove lips one of which, however, is said to be very small. In all the New-World Tylopoda examined, we could only ascertain the presence of one oesophageal groove lip.

In the figured cross-section of the oesophageal groove of the llama (Pl. 2, fig. 8) there is a small lateral continuation, but this is in no way a second lip. This lateral fold is an artefact resulting from fixation and imbedding of the material. This becomes clear by inspection of the whole complete structure of the oesophageal groove lip. After removal of the mucous membrane of the lip and the surrounding parts of the rumen, it can observed that there is only one lip without side-folds and no evidence of a second lip. As can be seen in Pl. 2, fig. 8, a layer of longitudinal muscle fibres extend into the lip from the left side (see fig.). At the other side of the lip there are only few longitudinal muscle fibres, which are situated nearer to the strong tunica muscularis of the stomach wall and none of them extend into the lip. (More detailed studies on these structures are given by Bohlken & Neteler).

Rumen The inner surface of the rumen of Ruminantia is thickly covered with papillae of differing size and form. These are largest in the section of the dorsal rumen sac which is bent towards the reticulum, and essentially smaller and weaker in the dorsal section of the dorsal rumen sac (Pl. 2, fig. 9). Such papillae are absent from the rumen of the Tylopoda, the mucous membrane of which is smooth (Pl. 2, fig. 10). As already pointed out in the Tylopoda the strong muscle pillars which divide the rumen of the Ruminantia are also absent. But in the rumen of the Tylopoda there are in the region of the glandular sacs strong muscle bands, between which the single glandular sacs are arranged in rows (Pl. 2, fig. 11). In the camel it was ascertained that the glandular sacs of the rumen are provided with glandular epithelium only in the lower part of their side-walls and at the bottom, whilst the glandular epithelium in the glandular sacs of the reticulum reaches the upper edge of the sacs, Hansen & Schmidt-Nielsen (1957). On the other hand we found in the New-World Tylopoda of the genus *Lama*, that the glandular sacs in the rumen are also provided with glandular epithelium right up to the topmost edge. Herein lies a difference then between the Old- and the New-World Typoloda.

Reticulum. The reticulum of the Ruminantia is distinguished by its honeycomb appearance (Pl. 2, fig. 12). The ground and walls of the honeycomb are covered with horny papillae. Grau (1955) and Schels (1956) have recently developed new conceptions regarding the function of the net-like cells in the reticulum of Ruminantia. The reticulum of the Tylopoda shows again a completely divergent structure. In one small area the mucous membrane is

smooth, but by far the greater part is taken up by glandular sacs (Pl. 2, fig. 13). In contrast to the glandular sacs of the rumen, those of the reticulum are covered by small eminencies at the bottom and on the side-walls, and these markedly increase the surface area. These eminencies are salient parts of the glandular sac walls, and are covered with the same glandular epithelium as is the remaining part of the wall. They are therefore not to be likened to the horny papillae in the reticulum and omasum of Ruminantia.

Omasum. The kidney-shaped omasum of the Ruminantia contains a large number of leaves of differing length, which reach far into the cavity (Pl. 3, fig. 14). These leaves or laminae are covered with horny papillae. In the Ruminantia the connection between the omasum and abomasum is clearly defined by two cross-folds at the side—the valvulae terminales. The two parts are sharply separated, one from the other (Pl. 3, fig. 15). The omasum of the Tylopoda is long and tube-shaped. The mucous membrane, a glandular epithelium, forms many folds of irregular height running along its whole length (Pl. 3, fig. 16). In the formalin-hardened stomach of the guanaco they are at most 5 mm high. In the oral third of the omasum there are some folds of greater strength, but they are no higher than the other folds. These thicker folds form an approximately net-like structure. Externally the omasum of the Tylopoda is not divided from the abomasum at all. From the inside, the line of division is made clear by the cessation of the folds of the omasum. Cross-folds, as in the Ruminantia, are not to be found (Pl. 3, fig. 17).

Abomasum. In the Ruminantia the abomasum is the only section of the stomach, in which the mucous membrane contains glands. The mucous membrane forms lengthwise folds (there are fourteen in the sheep) which are highest in the middle section of the abomasum (Pl. 3, fig. 18). The folds are of varying height, but there are only few which are small. The highest in the formalin-hardened stomach of the sheep measure 4 cm. The abomasum of the Tylopoda is very small. The mucous membrane of the adult animals has no folds; we observed folds only in foetal stomachs (Pl. 3, fig. 19). In the abomasum two areas of the mucosa may be distinguished even macroscopically. In the oral two-thirds of the abomasum there are the fundus glands, in the aboral third there are the pyloric glands. Here the naked eye can observe tightly arranged gastric pits (Pl. 3, fig. 20).

DISCUSSION

This comparison of the stomach of the Tylopoda with that of the Ruminantia leads to two conclusions :

(1) It is extremely difficult to find homologies between the divisions of the stomach of Ruminantia and those of the Tylopoda for the following reasons :

(a) The arrangement of the proventriculi in relation to the oesophagus and the oesophageal groove is different in these two groups.

(b) The oesophageal groove is different in construction. That of the Ruminantia has two lips, that of the Tylopoda has only one.

(c) The gross anatomy of the stomach of the Tylopoda, especially that of the omasum and abomasum differs greatly from that of the Ruminantia.

(d) The structure of the inner surfaces of all the divisions of the stomach is very different in Tylopoda and Ruminantia.

These are the main points which argue against the homologous nature of the compartments of the stomach in Tylopoda and Ruminantia. In order to reach a solution of this problem, detailed studies on the early embryonic development of the stomach of the Tylopoda would be necessary, such as those which have been undertaken on the stomach of Ruminantia, Pernkopf (1931). It seems likely that this is a case of parallel development in the phylogeny of the Tylopoda and the Ruminantia. This is confirmed by the second result of this comparison of the stomachs.

(2) Ruminating as a physiological process is closely connected with the anatomy of the stomach. It was pointed out, however, that there are a number of marked structural dissimilarities in the stomach of the Tylopoda and the Ruminantia.

(a) The three proventriculi of the Ruminantia have a mucous membrane which is covered with squamous stratified epithelium and is non-glandular. The epithelium of the reticulum and the omasum is covered with horny papillae. Gastric glands can only be found in the abomasum. In the Tylopoda, however, glandular epithelium also occurs in the proventriculi; this covers the glandular sacs of the rumen and the reticulum as well as the omasum.

(b) The glandular sacs in the rumen and the reticulum of the Tylopoda are not a result of an adaption to life in deserts; their purpose is not the storing of water, and they may have a digestive function. Though this function is still unknown, there is no doubt that, since the Ruminantia lack these anatomical peculiarities, the physiology of the digestion in the proventriculi may be different from that of the Tylopoda.

(c) In the omasum of the Tylopoda there are no laminae, which are typical for this compartment in the stomach of Ruminantia.

(d) The abomasum of the Tylopoda is conspicuously smaller, apart from the fact that the adult animals have no longitudinal folds.

These anatomical differences make it possible to surmise that the physiology of digestion in the stomach cannot be the same in the two groups. These considerations indicate too, that the faculty of ruminating has been acquired twice in the phylogeny of the Artiodactyla :—once by the Ruminantia in the narrower sense, and on the other occasion by the Tylopoda. To the taxonomist this means that although both the Ruminantia and the Tylopoda are ruminants the process of digestion may be different in both and, therefore, cannot be taken for a common physiological factor, which would be a justification for uniting the two groups. These results support the separation of the Tylopoda from the Ruminantia.

Other anatomical peculiarities of the Tylopoda indicate the same. These were listed for instance by Weber (1928) and Winge (1942). Only some of them need be mentioned here :

In contrast to the Pecora and Tragulina, the Tylopoda have permanent upper incisors and canines. They have neither horns nor antlers. In the Tylopoda the bones of the carpus and the tarsus are separate. The vertebral artery does not run through the transverse processes of the cervical vertebrae as it does with the other forms.

Previous authors (Cordier, 1893 ; Hilzheimer, 1916 ; and Pernkopf & Lehner, 1937) have already referred to similarities between the stomach of the Tylopoda and that of certain forms of the Suiformes. They especially mention the peccary (*Tayassu* Fischer, 1814). Perhaps the Tylopoda, with regard to their stomach, hold a position between the Suiformes and the Ruminantia. (See Bohlken & Neteler).

SUMMARY

The stomach of the Tylopoda differs fundamentally from the stomach of the Ruminantia in many details of its anatomy. From these anatomical differences it is concluded, that the physiological process of digestion may also be different. The results indicate, that the stomach compartments of the Tylopoda are not homologous with those of the Ruminantia, and that the faculty of ruminating has been acquired twice in the phylogeny of the Artiodactyla, once by the Ruminantia and independently by the Tylopoda. The results of the stomach comparison, like the palaeontological evidence, support the separate systematic position of the Tylopoda.

ACKNOWLEDGMENTS

I wish to express my gratitude to Professor Dr W. Herre, Director of the Institut für Haustierkunde in Kiel, and to Dozent Dr M. Röhrs for their kind permission to examine the material of their South-America-Expedition. For further material thanks are due to Mr C. Hagenbeck in Hamburg. I am also greatly indebted to B. Neteler, for his help with the dissection of the material and for cutting some material for histological examination, and to D. Bährens for assisting with the photographic work.

REFERENCES

Anthony, J. (1958). In : Discussion générale ayant suivi les rapports de MM. Frechkop et Lavocat. *Mammalia* **22** : 41–44.

Boas, J. E. V. (1890). Zur Morphologie des Magens der Cameliden und der Traguliden und über die systematische Stellung letzterer Abtheilung. *Morph. Jahrb.* **16** : 494–524.

Bohlken, H. & Neteler, B. Vergleichend-morphologische Studien am Magen der Tylopoden. (In preparation).

Colbert, E. H. (1955). *Evolution of the vertebrates*. New York–London.

Cordier, J. A. (1893). Recherches sur l'anatomie comparée de l'estomac des Ruminants. *Ann. Sci. nat. (Zool.)* (8) **16** : 1–128.

Ellenberger, W. & Baum, H. (1934). *Handbuch der vergleichenden Anatomie der Haustiere*. 18. Aufl. Berlin.

Frechkop, S. (1955). Sous-Ordre des Ruminants ou Sélénodontes. In : Grassé : *Traité de Zoologie* : **17**, Mammifères. Paris.

FRECHKOP, S. (1958). In : Discussion générale ayant suivi rapports de MM. Frechkop et Lavocat. *Mammalia* **22** : 41–44.

GRASSÉ (1955). *Traité de Zoologie* : **17**, Mammifères. Paris.

GRAU, H. (1955). Zur Funktion der Vormägen, besonders des Netzmagens, der Wiederkäuer. *Berl. Münch. Tierärztl. Wochenschr.* **68** : 271–275.

GREGORY, W. K. (1910). The orders of mammals. *Bull. Amer. Mus. nat. Hist.* **27** : 1–524.

HANSEN, H. & SCHMIDT-NIELSEN, K. (1957). On the stomach of the camel with special reference to the structure of its mucous membrane. *Acta anat.* **31** : 353–375.

HILZHEIMER, M. (1913). *Handbuch der Biologie der Wirbeltiere.* Stuttgart.

HILZHEIMER, M. (1916). Säugetiere. In : *Brehms Tierleben.* 4. Aufl. **4**, Leipzig–Wien.

LAVOCAT, R. (1958). Classification des Ongulés d'après leur origine et leur évolution. *Mammalia* **22** : 28–40.

PERNKOPF, E. (1931). Die Entwicklung des Vorderdarmes, insbesondere des Magens der Wiederkäuer. *Z. Anat. Entw.-Gesch.* **94** : 490–622.

PERNKOPF, E. & LEHNER, J. (1937). Vorderdarm. In : Bolk, Göppert, Kallius & Lubosch : *Handbuch der vergleichenden Anatomie der Wirbeltiere.* **3**. Berlin-Wien.

PETTER, F. (1956). La fin d'une longue erreur scientifique : Comment le Chameau resiste à la soif. *La Nature*, No. 3255 : 263–265.

ROMER, A. S. (1953). *Vertebrate paleontology.* 2. Edit. Chicago.

SCHELS, H. (1956). *Untersuchungen über Wandbau und Funktion des Netzmagens des Rindes. Diss. München* 52 pp.

SCHIMKEWITSCH, W. (1921). *Lehrbuch der vergleichenden Anatomie der Wirbeltiere.* Stuttgart.

SCHMIDT-NIELSEN, K., SCHMIDT-NIELSEN, B., HOUPT., T. R. & JARNUM, S. A. (1956). The question of water storage in the stomach of the camel. *Mammalia* **20** : 1–15.

SIMPSON, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* **85**, i–xvi, 1–350.

SISSON, S. & GROSSMAN, J. D. (1938). *The anatomy of the domestic animals.* 3rd Edit. Philadelphia–London.

YOUNG, J. Z. (1950). *The life of vertebrates.* Oxford.

WEBER, M. (1928). *Die Säugetiere.* 2. Aufl. **2**. Jena.

WINGE, H. (1942). *The interrelationships of the mammalian genera.* **3**, *Ungulata, Cetacea* Kobenhavn.

EXPLANATION OF THE PLATES

PLATE 1

Fig. 1.—Diagram of the stomach in Ruminantia (above) and the stomach in Tylopoda (below). ab. abomasum ; d. duodenum ; g. oesophageal groove ; o. oesophagus ; pa. omasum ;. re. reticulum ; ru. rumen. (From Boas, 1890).

„ 2.—Stomach of an adult guanaco in about the same arrangement as in the diagram Fig. 1 (below).

„ 3.—Stomach of a foetus of domestic ox in about the same arrangement as in the diagram Fig. 1 (above).

„ 4.—The stomach of the adult guanaco (Fig. 2) in another view. To the left on the rumen the large glandular sac area, to the right at the margin the small one.

„ 5.—Oesophageal groove in the stomach of an adult sheep. To the left the opening of the oesophagus, to the right the reticulo-omasal orifice.

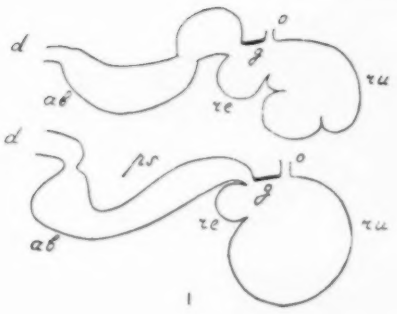
„ 6.—Cross-section of the oesophageal groove of the sheep showing the two lips. Hemalum-eosin stain.

„ 7.—Oesophageal groove in the stomach of an adult llama. To the left the opening of the oesophagus, to the right the reticulo-omasal orifice. Note the single lip.

PLATE 2

Fig. 8.—Cross-section of the oesophageal groove of the llama. Note the single lip. Hemalum-eosin stain.

„ 9.—Papillae in the rumen of the sheep. To the left in that part of the dorsal rumen sac, which is bent towards the reticulum, to the right in the dorsal section of the dorsal rumen sac.



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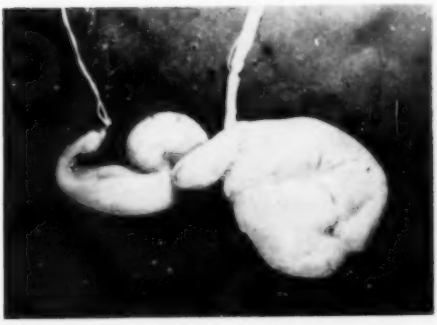

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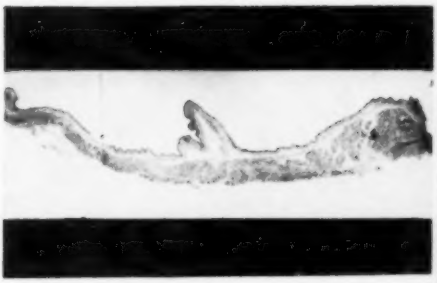
The stomach and the systematic position of the Tylopoda.



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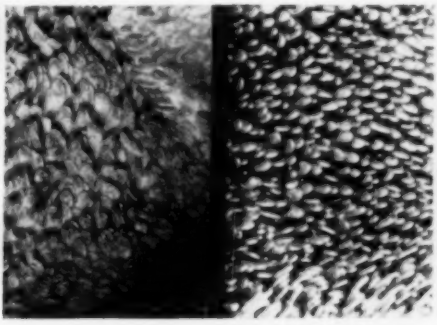

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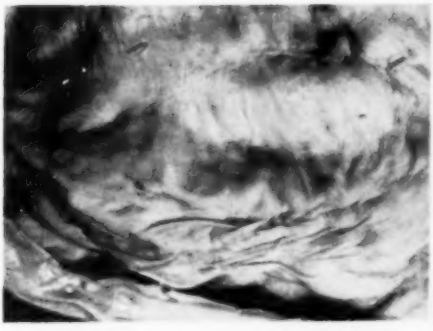

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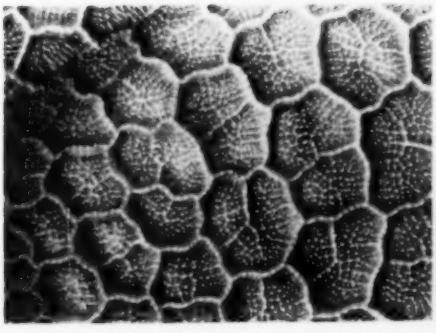

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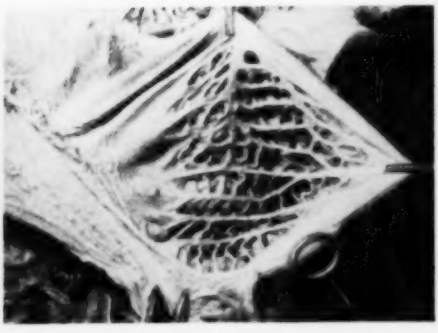

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The stomach and the systematic position of the Tylopoda.

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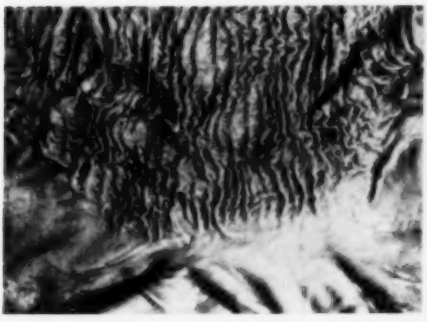

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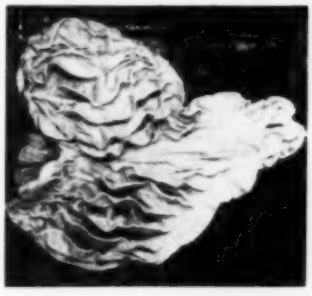

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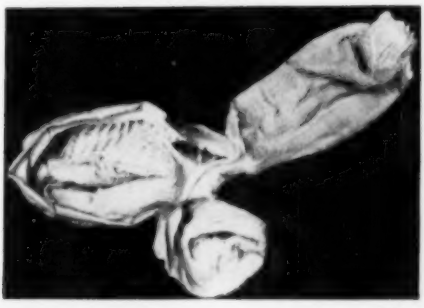

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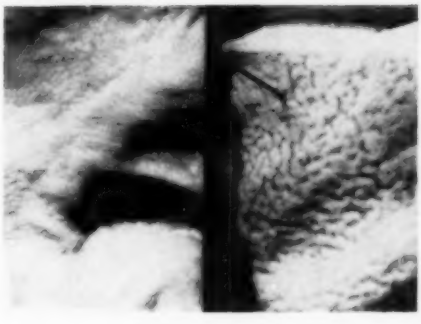

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The stomach and the systematic position of the Tylopoda.

Fig. 10.—Mucous membrane in the rumen of the guanaco.
„ 11.—The large glandular sac area in the rumen of the guanaco.
„ 12.—A piece of the mucous membrane of the sheep's reticulum.
„ 13.—Reticulum of the guanaco with the glandular sacs.

PLATE 3

Fig. 14.—Cross-section of the omasum of the sheep.
„ 15.—Boundary between omasum and abomasum in the sheep.
„ 16.—Omasum of the guanaco.
„ 17.—Boundary between omasum and abomasum in the llama.
„ 18.—Abomasum of the sheep.
„ 19.—Stomach of a foetus of vicuna (head-and-body-length of foetus 625 mm.). In the abomasum there are thick longitudinal folds (above to the right).
„ 20.—Mucous membrane in the abomasum of the guanaco. To the left the region of fundus glands, to the right the region of pylorie glands.

EARLY DEVELOPMENT OF *LIMNOCNIDA VICTORIAE* GUNTHER (LIMNOMEDUSAE)

BY

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[Communicated by Professor H. Munro Fox, F.R.S.—Accepted 10th November 1959]

(With 1 plate)

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INTRODUCTION

Of the two known genera of freshwater medusae, *Craspedacusta* has the wider distribution and has been recorded from North and South America, Europe, Asia and Australia, but not from Africa. *Limnocnida*, on the other hand, is apparently confined to Africa and southern India.

The medusae of both genera were first discovered in the 1880's. The hydroid generation of *Craspedacusta sowerbii* Lankester was found in 1885 and the details of the life history were described by Payne (1924, 1926). It was not, however, until 1954 that Bouillon first discovered the hydroid of *Limnocnida* attached to reeds in Lakes Tanganyika and Mohasi, observed their development from fixed elongated larvae and the production of medusae by budding from the hydroid. He has recently published a comprehensive monograph on the genus *Limnocnida* including original observations on structure, histology and life history (Bouillon, 1957). But the development of the hydroid from the egg remains to be described and is the subject of the present paper.

In a preliminary note (Beadle & Thomas, 1957) the species was referred to as *Limnocnida tanganyicae*, but we now follow the classification proposed by Bouillon (1957) and refer our specimens to *L. victoriae*, whose medusae differ from those of *L. tanganyicae* in not reproducing by budding and in having shorter and more numerous tentacles.

MATERIAL

The medusae were caught at the head of the Murchison Gulf in the north-eastern corner of Lake Victoria, between Kaazi and Port Bell. The depth of the water is mostly less than 7 m. and it is generally rather turbid.

The observations were too infrequent to warrant any definite conclusions regarding the factors responsible for the swarming of the medusae in the surface waters. The medusae were recorded in mid-November 1953 and in September 1956 and in both periods they were in evidence for about a week. In 1958 they were found several times between July 20th and Sept. 1st, and it seemed

as if they could have been caught at any time during that period. The most that can be said is that they have not been seen by us during the period January-March which normally has least rain.

The medusae were mainly to be found in sheltered water, as in the lee of an island, and varied greatly from time to time both in location and numbers. They were most abundant near the surface towards sunset, which is almost invariably a calm period. The collections always contained specimens of different sizes and there was therefore no evidence of a sudden outburst of budding of medusae from the hydroids.

It was found by chance during the second period (22nd Sept. 1956) that the larger medusae produced eggs and sperm when put into dishes in the laboratory. This was repeated on three occasions during the period July–September 1958, and it seems likely that eggs and sperm could always be obtained in this way. They are, however, very small and invisible amongst the debris, to the naked eye or even under a hand lens, and are thus easily overlooked.

DEVELOPMENT FROM EGG TO HYDROID

The eggs and sperm shed in the laboratory were observed under the microscope. The following is the approximate timetable of events recorded on the first occasion and confirmed twice subsequently. The temperature was 20–23°C.

Up to 2 hours	Uncleaved eggs (Plate I A).
4 hours	2 and 4 cell stages. (Plate I B and C)
16 ,,	Spherical, not yet motile larvae with few cilia.
28 ,,	Spherical, motile, ciliated planulae. (Plate I E).
42 ,,	Planulae beginning to settle, lose cilia and elongate.
60 ,,	Attached elongated larvae (Plate I F and G).
5 days	Characteristic flask-shaped hydroids. (Plate I H–J).

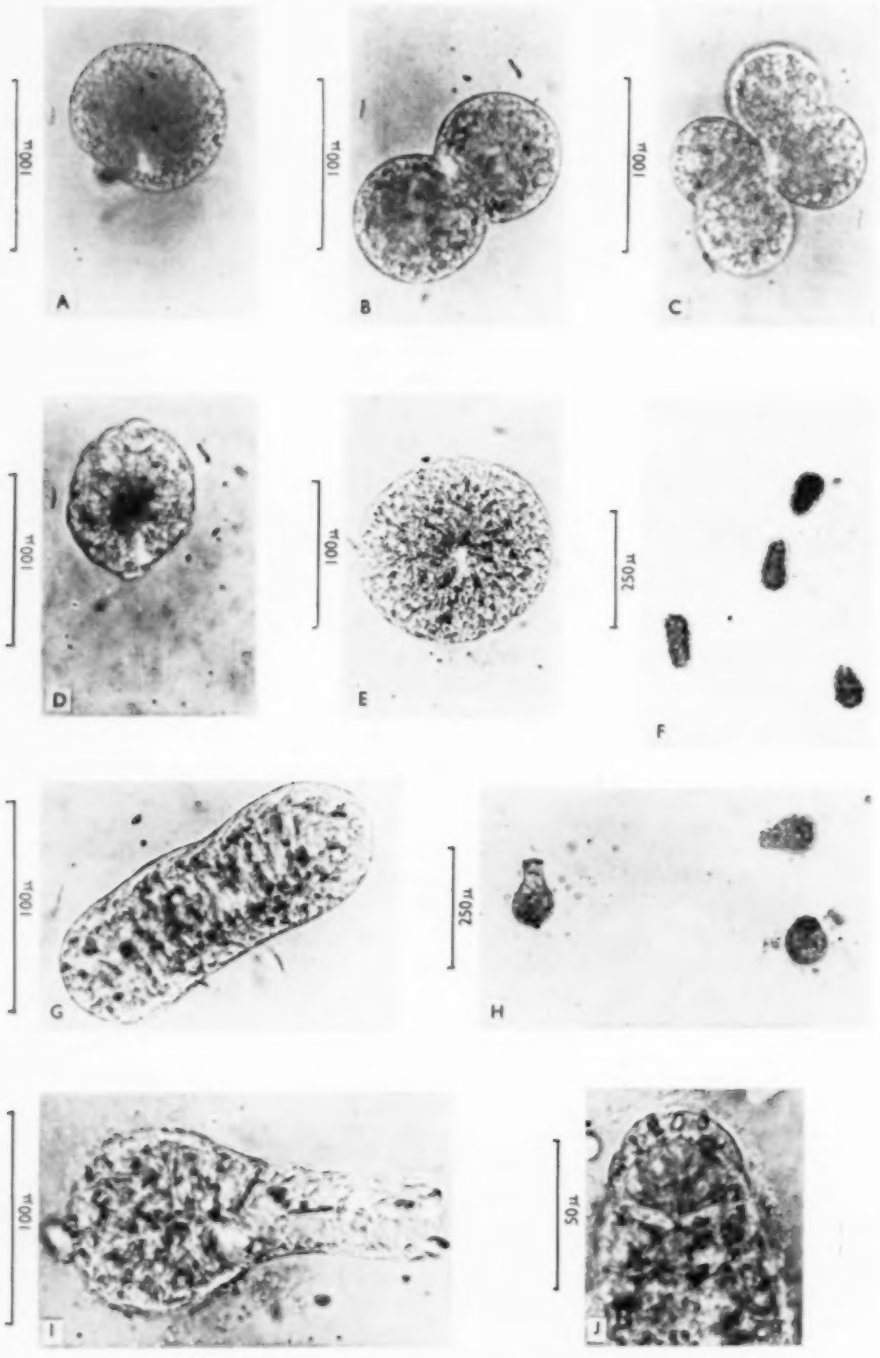
The approximate dimensions of these stages is given in the legend of the plate. They are considerably smaller than (about one-fifth) the corresponding stages of *Craspedacusta sowerbii* (Dejdar, 1934). The diameter of the eggs of *Craspedacusta* is 540–580 μ, that of *Limnocnida* is 90–100 μ. The length of the hydroid of *Craspedacusta* is 660–1,200 μ, that of *Limnocnida* 190–200 μ. This difference is presumably one of the reasons why, after discovery of the medusae, it was seventy years before the hydroid of *Limnocnida* was found but only five in the case of *Craspedacusta*.

It is to be noted that the course of development from egg to hydroid is otherwise very similar in the two genera. They both produce spherical, motile, ciliated planulae which settle before elongating. We did not, however, find that the rate of cleavage was markedly unequal after the 2-cell stage (Plate I F and G), as found by Payne (1926) for *Craspedacusta*.

REFERENCES

Beadle, L. C. & Thomas, I. F. (1957). The African freshwater jellyfish *Limnocnida tanganyicae*. *Nature, Lond.* **179** : 110.

Bouillon, J. (1957). Etude monographique du genre *Limnocnida* (Limnomeduse). *Ann. R. Soc. Zool. Belg.* **87** : 254–500.



Early development of *Limnocnida victoriae*.

DEJDAR, E. (1934). Die Süsswassermeduse *Craspedacusta sowerbii*. *Z. Morph. Ökol. Tiere.* **28** : 595–691.

PAYNE, F. (1924). A study of the freshwater medusa *Craspedacusta ryderi*. *J. Morph.* **38** : 387–430.

PAYNE, F. (1926). Further studies on the life history of *Craspedacusta ryderi*, a freshwater hydromedusan. *Biol. Bull. Woods Hole* **50** : 433–42.

EXPLANATION OF THE PLATE

A to D—High power appearance of cleavage stages.

A, single egg ; B, first cleavage in progress ; C, 4-celled stage ; D, morula with increasing number of cells.

E to J—Development of hydroid.

E, Planula flattened under coverslip to show cells ; F, Stages in elongation ; G, Elongation complete ; H, Hydroids ; I, Single hydroid ; J, Mouth of hydroid with cnidoblast cells.

GROWTH AND FORM OF THE BRINE SHRIMP *ARTEMIA SALINA* (L.)

BY

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[Accepted 10th November 1959]

(With 5 figures in the text)

The growth and form of *Artemia salina* (L.) from three different localities has been investigated under standard conditions of temperature and feeding, in two concentrations of brine.

Parthenogenetic females from southern France have a higher growth rate than females of the bisexual Californian stock ; the growth rate of sexually mature females is greater than that of males. The extent to which growth is influenced by the salinity of the medium varies with the sex of the animal and the stock from which it is derived.

Changes in body proportions occur with increase in size of *Artemia* ; in particular, the abdomen becomes relatively longer. Brine shrimps from different localities, reared through several generations under standard conditions, are morphologically distinct.

Body form is also influenced by the salinity of the external medium, but certain intrinsic factors, in particular the sex and genetic constitution of the animal, modify the effects of external salinity.

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INTRODUCTION

Much has been written about the variations in form of the brine shrimp, *Artemia salina* (L.), in relation to the salinity of the medium in which it lives. This has been the subject of many investigations and is an aspect of the biology of *Artemia* most extensively studied. Numerical data on the variations observed, however, are either lacking or inadequate. Changes in body form under the influence of certain extrinsic factors, in particular the salinity of the medium, have been observed and occasionally measured without reference to the possible influence of intrinsic factors on body form.

Since the form of an animal is the result and consequence of growth, size must be regarded as an important intrinsic factor likely to influence body form. The object of the work described in this paper is to provide adequate numerical data on the variations in form of adult *Artemia*, cultured under standard conditions, in relation to size and sex, the stock from which the animals have been derived and the salinity of the external medium.

This work formed part of a thesis approved by the University of London for the degree of Ph.D.

MATERIAL AND METHODS

Eggs of *Artemia* were obtained from salt works in Europe, North Africa and America. From these, cultures were maintained of animals derived from the following sources, La Palme (Aude, southern France), Arzeu (Algeria) and San Diego (California). In agreement with Linder (1941) only a single species of *Artemia*, namely *A. salina* (L.), is recognised in this paper. The animals from the localities listed above will be referred to as La Palme, Algerian and Californian stocks respectively. Brine shrimps from La Palme are parthenogenetic and diploid while those from California are bisexual and diploid. The stock from Algeria is bisexual and probably diploid although the number of chromosomes has not been counted. The shape of the head and early development of the metanauplius of this stock is similar to that described by Stella (1933) as characteristic of bisexual diploid brine shrimps.

Stock cultures of *Artemia* were maintained in sea water ($S‰35$) and in a concentrated brine ($S‰140$) in a constant-temperature room at 25°C. A marine alga, *Dunaliella tertiolecta* Butcher 1959, was given as food. This was cultured in ' Miquel-Allen sea water ' (Allen & Nelson, 1910).

In all experiments on growth and form the animals were reared under constant culture conditions with controlled feeding. The method used was similar to that of Fox, Gilchrist & Phear (1951) for the controlled feeding of *Daphnia*. The density of a suspension of *Dunaliella* in the experimental brine was measured with a Medical Research Council greywedge photometer using a red filter. At the start of the experiments the *Dunaliella* suspension was adjusted to an optical density of about 0·15. More *Dunaliella* was added daily to restore the optical density to 0·15.

The concentration of brine shrimps in the experimental vessels was adjusted to the size of the individuals. Three concentrations were used in relation to three approximate size groups as shown below :—

Artemia per 100 ml. brine	length, mm.
10	hatching to 3·0
2	3·0 to 6·0
1	over 6·0

Concentrated brine ($S‰140$) was obtained by dissolving commercial sea salt in sea water and filtering the solution. The salinity of the experimental brines was checked regularly by titration with a standard solution of silver nitrate (Harvey, 1955).

Under the culture conditions described females of *Artemia* are viviparous and actively swimming nauplii are liberated from the brood pouch of the parent. These nauplii were collected from females reared in the experimental brines and transferred to dishes containing a volume of brine appropriate to the number of nauplii available, to give a concentration of one nauplius per 10 ml. of brine. With increasing size of the animals the concentration was adjusted and controlled feeding was given throughout the experiments as described above. In experiments on variation in body form, the animals

used were derived from parents which had been reared in the experimental brines for at least two generations.

A number of animals was withdrawn from the experimental vessels at frequent intervals during the experiments. These individuals were lightly narcotised, measured and on complete recovery from narcosis were returned to their respective experimental dishes.

All measurements were made on animals lightly narcotised with chloroform. As suggested by Lochhead & Lochhead (1941) a few drops of chloroform in about 10 ml. of brine was found to be the most satisfactory narcotic. In this the animals remain motionless for a few minutes but the heart continues to beat and recovery is complete within ten minutes. Narcotised animals were placed ventral side down on a microscope slide and supported in a little of the experimental medium. In males the large second antennae were bent forward to extend in front of the head and in females with a well developed brood pouch, the measurements were made with the animal lying in a cavity slide. These precautions insured that the animals lay horizontally on the slide. Total length from the anterior margin of the head in front of the ocellus to the base of the caudal furca was measured with a Vernier scale on the mechanical stage of the microscope. Similarly, the length of the abdomen was measured from and including the first genital segment to the base of the caudal furca. With a calibrated eye-piece micrometer the abdomen width was measured at the level of the posterior termination of the heart also the length of the caudal furca from base to tip.

GROWTH

Previous work

Few studies have been made on the growth of *Artemia*. It is stated by a number of authors (Martin & Wilbur, 1921 ; Heath, 1924 ; Bond, 1933 ; Warren, 1938) that the adult size of *Artemia* varies inversely with the salinity of the external medium and in laboratory bred animals sexual maturity is attained three to four weeks after hatching. According to Jensen (1918) *Artemia* from the Great Salt Lake, reared in the laboratory at room temperature in brine of unspecified salinity, is sexually mature 18 to 21 days after hatching. Barigozzi (1939) measured the average time of development, from hatching to sexual maturity, in three populations of brine shrimps cultured in the laboratory at 18 to 20°C in an artificial sea water. No difference in time of development in the different populations was observed ; the bisexual animals from America and the parthenogenetic females from the south of France and north Italy all became sexually mature 22 to 28 days after hatching.

In these experiments no actual measurements of length appear to have been made and neither the temperature nor the amount of food given controlled. More precise experiments on growth rate have been made by Weisz (1946), who was primarily interested in segment formation in relation to size and shape of *Artemia*. According to Weisz (1946) the rate of development of *Artemia* from hatching to sexual maturity is directly related to the salinity of the external medium. Animals reared in dilute brine (S‰ 30) became sexually mature about 32 days after hatching while those in more

concentrated brine (S‰115) were sexually mature in about 22 days. In both media the animals were fed on a sea-water-yeast suspension.

The studies of Barigozzi (1939) and Weisz (1946) give no information on the growth of *Artemia* after sexual maturity nor of the relative growth rates of males and females. In the present investigation, therefore, experiments were made to determine the growth rates of male and female *Artemia* under standard conditions and in two concentrations of brine.

Factors influencing growth

In Fig. 1 the growth of males and females of the Californian stock and females of La Palme stock of brine shrimps is compared in two concentrations of brine. Each value represents the mean length of thirty individuals. In

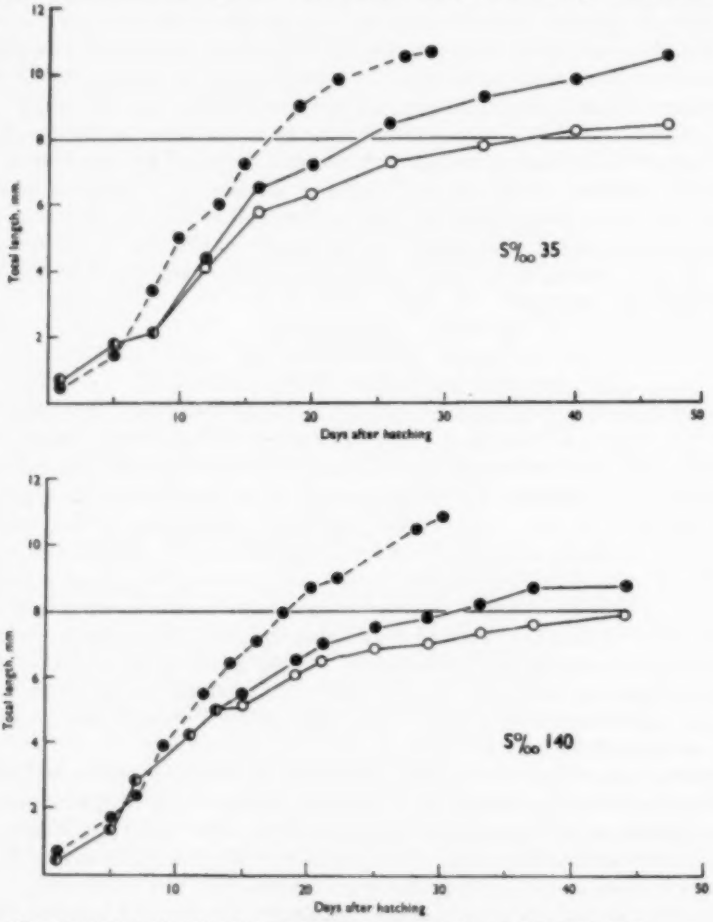

Fig. 1.—Growth of *Artemia salina* in two different concentrations of brine at 25°C.
●——● females, Californian stock; O——O males, Californian stock
●- - -● females, La Palme stock.

both media the animals became sexually mature 15 to 17 days after hatching.

By comparing the time taken by *Artemia* to reach a total length of 8 mm., it is clear that parthenogenetic females of La Palme stock have a higher rate of growth in both media than females of the bisexual Californian stock. This difference is already established before sexual maturity is attained. Likewise, in both media the growth rate of sexually mature females is greater than that of males, the difference being more marked in sea water. This confirms an observation made by Artom (1907 a) that in equal concentrations of brine males have a shorter total length than females.

The extent to which growth is influenced by the salinity of the external medium varies with the stock and sex of *Artemia*. When the growth of females of the Californian stock is compared in the two media it is found that the growth rate is greater in sea water than in the more concentrated brine. In males the difference in growth rate in the two media is less obvious but if the mean lengths of animals 33 days old are compared statistically, it is found that males in sea water are significantly longer than males in the more concentrated medium. With 58 degrees of freedom and 't'$=2{\cdot}36$, the probability that the difference is due to chance is less than 5 per cent. Thus, in both males and females of the Californian stock the size of sexually mature individuals is inversely related to the salinity of the external medium. No significant difference was found in the rate of growth of parthenogenetic females reared in the two different media. Observations on natural populations of brine shrimps at La Palme have shown that the average length of *Artemia* is inversely related to the salinity of the external medium (Gilchrist, 1956). This difference in growth rate between laboratory bred and natural populations may be related to the decrease in available food as the salt concentration of the natural brine reservoirs increases. In laboratory cultures the same amount of food was available in the two different concentrations of brine.

It has been shown in Fig. 1 that the size of adult brine shrimps of the Californian stock varies inversely with the salinity of the external medium. The dissolved oxygen content of brine also varies inversely with the salt concentration. It is known that the growth of females of the Californian stock is retarded by lack of dissolved oxygen (Gilchrist, 1954). The growth rate of males, however, is not significantly slower in oxygen deficient water. It may be, therefore, that the smaller size of adults of the Californian stock in concentrated brine is in part, if not entirely, an effect of the low dissolved oxygen content of the medium. Whether due directly to the salt concentration or the dissolved oxygen content, the effect is more marked in females than in males of *Artemia*.

The conclusion of Weisz (1946) that up to the time of sexual maturity the growth rate of *Artemia* varies directly with the salinity of the external medium, seems to contradict the findings of other workers. Eliassen (1952) has shown that the oxygen consumption of nauplii and immature stages of *Artemia* is higher in sea water than in more concentrated brine ($S‰50$). Thus, according to Eliassen (1952) the metabolism of nauplii of *Artemia* is inversely related to the salinity of the medium and according to Weisz (1946) the growth rate of nauplii is directly related to the salinity of the medium. It should be

pointed out, however, that the growth rate of nauplii in the sea-water-yeast suspension used by Weisz (1946) was slow. Animals became sexually mature about 32 days after hatching in the least concentrated medium ($S‰30$) at 21 to 22°C. In my own experiments, *Artemia* cultured in sea water at 25°C and fed on *Dunaliella* is sexually mature 15 to 17 days after hatching. This suggests that the sea-water-yeast suspension is less satisfactory food for *Artemia* than the green alga.

BODY FORM

Previous work

About the middle of the nineteenth century several new species of *Artemia* were described from different parts of the world. Important morphological characters used in the determination of species were the size of the caudal furca and the number of setae on it. The variability of these characters under the influence of the salinity of the external medium was first demonstrated by Schmankewitsch (1875, 1877). He showed that with increasing salinity the abdomen of *Artemia* grows relatively longer and narrower, the caudal furca is reduced and bears fewer setae and the epipodite or bract of the limbs becomes larger. Further observations on these modifications of form have been made by a number of authors, in particular Bateson (1894), Anikin (1898), Samter & Heymons (1902), Kellogg (1906) and Artom (1907 a, 1907 b).

There is considerable disagreement among the above authors as to the cause and extent of the modifications of body form of *Artemia*. A complete review of their findings is given by Abonyi (1915). One of the main criticisms which must be made about this early work is that numerical data are either lacking or incomplete and many of the observations were made only on natural populations of brine shrimps in media subject to considerable fluctuations in concentration. Extensive measurements were made, however, by Artom (1907 a) on brine shrimps from natural populations near Cagliari, Sardinia. In any one concentration of brine the body proportions are given of animals differing considerably in size and Artom attempts to compensate for this by correcting all measurements to a standard length of thorax of 3·6 mm. This is valid only if it has been shown that there is no variation in body proportions with size ; Artom gives no evidence that body proportions remain constant over the size range of animals investigated.

Abonyi (1915) attempts to simplify the problem by suggesting that the density of the brine in which *Artemia* occurs is ' specific ' ; a particular variety of *Artemia* , having certain characteristic features, is more or less identifiable by the density of the brine in which it is found. Unlike most authors Abonyi (1915) considers that it is the viscosity and not the salt content of the brine which is the important factor influencing body form of *Artemia*.

The observations of the authors so far mentioned were made on brine shrimps from populations in Europe and Asia. More recently Bond (1933), Kuenen (1939) and Weisz (1946) have studied the form of *Artemia* from California. Bond (1933) concludes from observations on natural populations and on laboratory bred animals that the Californian brine shrimp remains constant in body form whatever the salinity of the external medium. Both

Kuenen (1939) and Weisz (1946) support these conclusions but it should be pointed out that Kuenen (1939) gives no numerical data and Weisz (1946) studied animals only from the time of hatching to sexual maturity. Further, in his experiments on laboratory bred animals Bond (1933) compares the body proportions of large animals in dilute brine with those of smaller animals in concentrated brine.

It is clear from this outline of previous work that no attempts have been made to investigate changes in body form during the growth of *Artemia* under constant conditions. It seems that this should constitute a preliminary study to the investigation of changes in body form in relation to the salinity of the external medium. In the present investigation, therefore, variations in body

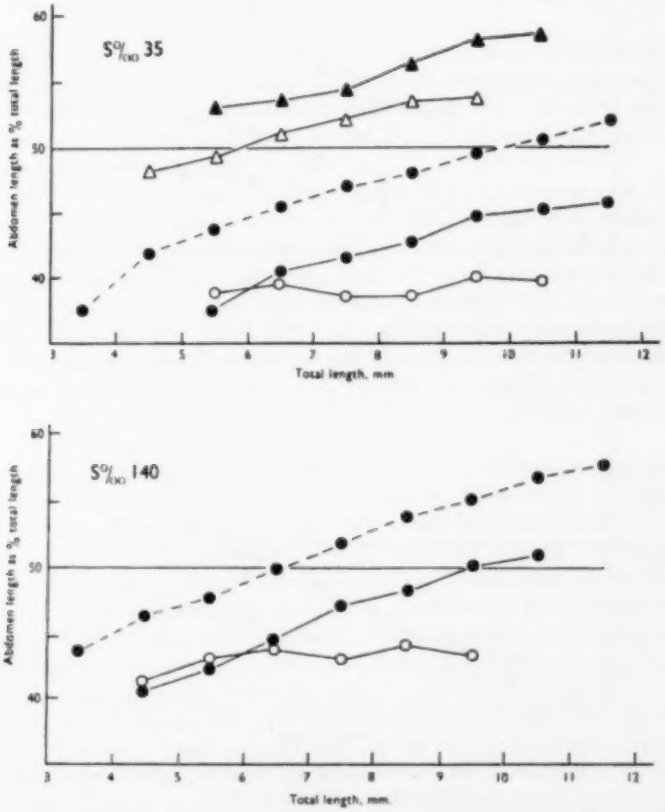

Fig. 2.—Length of abdomen, as percentage of total length, in relation to size, sex and stock of *Artemia* reared in two different concentrations of brine at 25°C.

●———● females, Californian stock ; O———O males, Californian stock

● - - -● females, La Palme stock

▲———▲ females, Algerian stock ; Δ———Δ males, Algerian stock.

form in relation to size, sex and stock of *Artemia* have been studied as well as variations in relation to external salinity.

Factors influencing body form

The results of these investigations are shown in Figs. 2 to 5. Each value represents the mean of measurements made on a number of animals ; the average number measured in each size group was thirty-three.*

The influence of certain intrinsic factors on the length and width of the

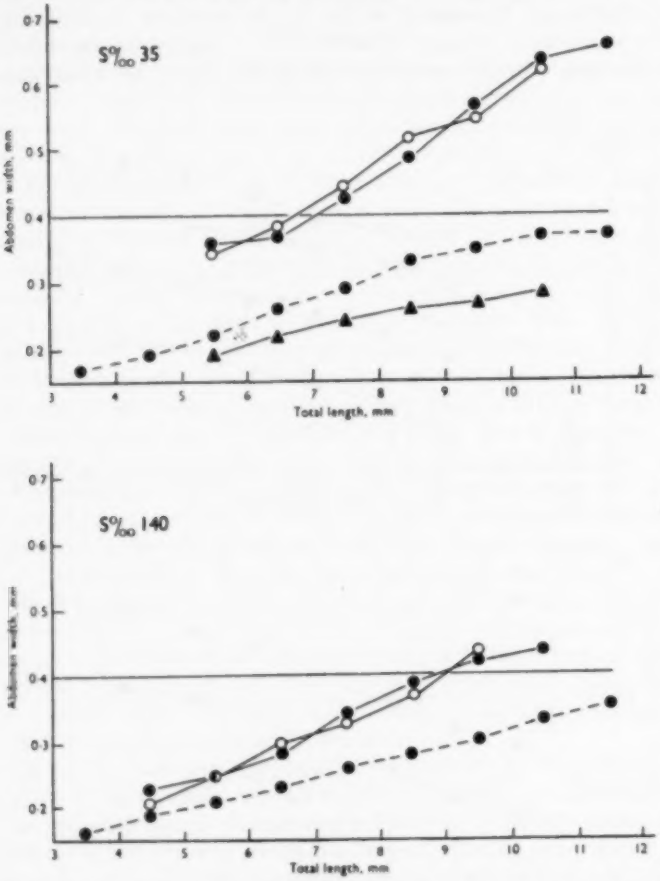

Fig. 3.—Width of abdomen in relation to size, sex and stock of *Artemia* reared in two different concentrations of brine at 25°C.

●——● females, Californian stock ; O——O males, Californian stock

● - - -● females, La Palme stock

▲——▲ females, Algerian stock.

* Detailed numerical data relating to these figures can be found in a thesis entitled "The metabolism of *Artemia salina* (L.)" in the Library of the University of London, together with data on body form of brine shrimps from Utah and Sardinia.

abdomen of *Artemia* and the length and setation of the caudal furca will be considered first. In females the abdomen becomes relatively longer as the total length of the animal increases (Fig. 2). This is so in the three stocks of brine shrimps investigated. For any particular length of female, however, the abdomen length as a percentage of total length is not the same in females from different stocks. In both experimental brines females of the Californian stock have a shorter abdomen than those of the same total length from La Palme. Likewise, females of La Palme stock have a shorter abdomen than those of the same total length from Algeria when reared in the same medium.

The abdomen of males of *Artemia* is shorter than that of females of the same total length reared in the same medium. The relative length of abdomen of males of the Californian stock remains constant over the size range investigated ; it does not become relatively longer as the total length of the animal increases.

The width of the abdomen increases with increase in total length of males and females of *Artemia* (Fig. 3). In animals of the same length the abdomen of males and females of the Californian stock is significantly broader than that of La Palme and Algerian animals. There is no significant difference in the width of abdomen of males and females.

The caudal furca of *Artemia* becomes longer with increase in size of males and females (Fig. 4). Females have a shorter caudal furca than males of the same total length reared in the same medium. Brine shrimps of the Algerian stock have a much shorter caudal furca than those of the other stocks investigated. In Fig. 5 it can be seen that the shorter furca of the Algerian animals bears fewer setae than the longer furca of La Palme and Californian animals. Likewise, the caudal furca of females, as well as being shorter than that of males, tends to bear fewer setae. This is well marked in the Algerian animals but less so in the Californian stock. Clearly, the number of setae per furca is related to the length of the furca.

It is well known that the body form of *Artemia* is influenced by extrinsic environmental factors, in particular the salinity of the external medium. It has already been shown in Fig. 1 that the effect of external salinity on the growth of *Artemia* is influenced by certain intrinsic factors. Since growth and form are intimately related it is not surprising to find that the effects of the salinity of the medium on body form are also modified by intrinsic factors.

In concentrated brine the abdomen of *Artemia* is longer and narrower than in animals of the same size and stock reared in sea water (Figs. 2 and 3). It is seen, however, that Algerian brine shrimps reared in sea water have a much longer and thinner abdomen than Californian animals of the same size reared in concentrated brine. Thus, the influence of the external medium is modified by the genetic constitution of the animals.

The caudal furca of *Artemia* reared in concentrated brine is shorter than that of animals of the same size and stock reared in sea water (Fig. 4). In La Palme stock the number of setae on the caudal furca is reduced in animals reared in concentrated brine but in the case of the Californian stock there is no significant difference in the number of setae on the furca of animals reared in the two different media (Fig. 5).

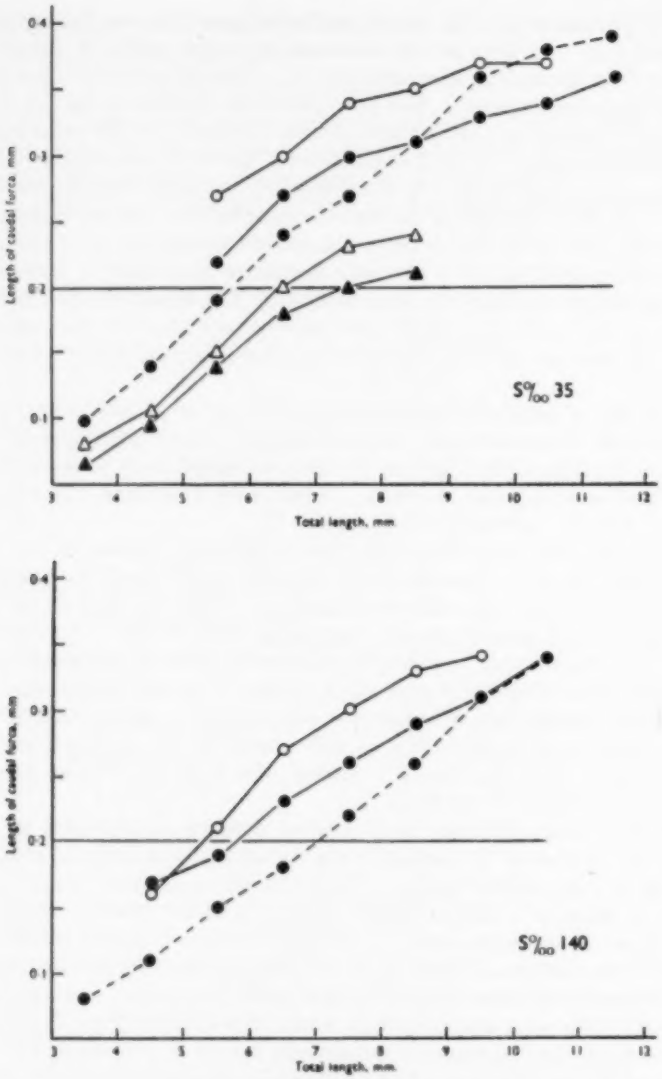

Fig. 4.—Length of caudal furca in relation to size, sex and stock of *Artemia* reared in two different concentrations of brine at 25°C.

●———● females, Californian stock ; O———O males, Californian stock
● - - -● females, La Palme stock
▲———▲ females, Algerian stock ; Δ———Δ males, Algerian stock.

DISCUSSION

It is clear that one cannot generalise about the influence of the external salinity on the body form of *Artemia*. Form is influenced by a number of

intrinsic factors when animals are reared under standard conditions ; it varies with size, sex and stock of animal. It seems, as first suggested by Bateson (1894), that each locality has its own particular pattern of *Artemia*. Under the same culture conditions animals from the western United States have a body form which differs significantly from that of animals from North Africa.

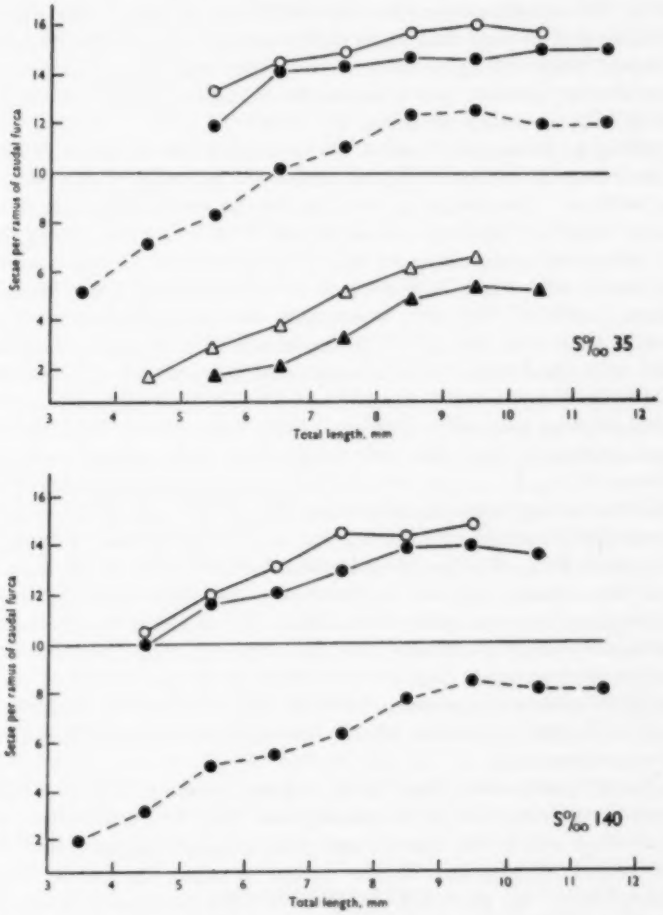

Fig. 5.—Number of setae per ramus of caudal furca in relation to size, sex and stock of *Artemia* reared in two different concentrations of brine at 25°C.

●——● females, Californian stock ; O——O males, Californian stock
●- - -● females, La Palme stock
▲——▲ females, Algerian stock ; Δ——Δ males, Algerian stock.

In the latter the abdomen is longer, narrower and bears a shorter caudal furca with fewer setae than the abdomen of animals of the same length and sex from

California when reared under the same conditions. Brine shrimps from south-west France seem to be intermediate in form between the two extremes described.

It was first suggested by Abonyi (1915) and later by Thompson (1942) that the density of the medium in which *Artemia* lives is ' specific ' to a particular body form ; the stronger the brine the relatively longer and thinner the abdomen. This suggestion is not supported by the results of my experiments. In Figs. 2 to 5 it is seen that both males and females of the Algerian stock reared in sea water (S‰35) have a markedly longer and thinner abdomen bearing a shorter and less setose caudal furca than animals of the Californian stock reared in concentrated brine (S‰140).

According to Bond (1933) brine shrimps from the western United States do not show any modification of form under the influence of the salinity of the external medium. He compared the ratio of the length of thorax to abdomen in *Artemia* reared in different concentrations of brine. The average length of animals measured covers a wide range ; those reared in sea water had an average length of 9·6 mm. while those in concentrated brine (S‰160) had an average length of 7·1 mm. Since there was no difference in the ratio of length of thorax to abdomen in these two groups of animals Bond (1933) concludes that Californian brine shrimps are not variable in form under the influence of the external salinity and thus differ in this respect from European and North African animals. It has already been shown from the results of my own experiments that this ratio itself varies with the size of the animal. By reference to Fig. 2 it can be seen that a female brine shrimp of the Californian stock 9·6 mm. in length reared in sea water has an abdomen which is 45 per cent. of the total length of the animal. A female 7·1 mm. in length reared in concentrated brine (S‰140) has an abdomen which is about 46 per cent the total length of the animal. Thus it might appear that there is no difference in the relative length of the abdomen of females reared in two different media. It is only when the factor of size is taken into account and animals of the same total length are compared that the real influence of the salinity of the medium on body form becomes apparent. Brine shrimps of the western United States, like those of Europe and North Africa, are variable in form under the influence of the external medium.

In a recent publication Baid (1959) expresses the view that *Artemia salina* is a neotenous form which metamorphoses into *A. milhauseni* when the concentration of salt in the water is raised to saturation point : in dilute media *Artemia* breeds as a larva. If the author is using the terms ' larva ' and ' metamorphosis ' as generally applied to the Crustacea, then the above suggestion cannot be accepted. *Artemia* in sea water, a dilute medium for brine shrimps, possesses all the morphological features characteristic of adults of the genus, including the secondary sexual characters of males. Further, the numerical data relating to body form presented by Baid are difficult to interpret since the author confuses length with breadth and recognises in *Artemia* an abdomen and a post-abdomen but, apparently, no thorax. Clearly, the views expressed by Baid (1959) cannot be discussed further until adequate data are presented.

There is an extensive literature describing varieties, biotypes and races of *Artemia* and the cytological and biological characteristics of these (for references see Daday, 1910 ; Artom, 1931 ; Gross, 1932 ; Stella, 1933 ; Goldschmidt, 1952 ; Barigozzi, 1957). It is not proposed to embark upon a discussion of this subject in the present paper, but it should be recalled that North African and Californian brine shrimps, cultured under standard conditions, are morphologically distinct and yet both populations appear to consist of bisexual diploid individuals. Further, males and females of these two populations will not interbreed. It seems advisable, however, in the absence of precise morphological characters on which to separate species, that only a single species within the genus *Artemia* should be recognised. Kuenen (1939) makes a tentative suggestion that two species of brine shrimp can be distinguished, *Artemia salina* (L.) and *A. gracilis* Verrill. The former is recognised by the presence of two lateral hairs on each abdominal segment and by the fact that body form is variable under the influence of the salinity of the external medium. European and North African brine shrimps would belong to this species. Californian animals, on the other hand, would belong to the second species, *A. gracilis* characterised by the absence of the two lateral hairs on each abdominal segment and the constancy of body form in media of different salt concentration. This suggested separation into two species cannot be supported. It has been shown in the present paper that the body form of Californian brine shrimps varies with the external salinity and, on examining animals from my cultures of this stock, two lateral hairs are found to be present on each abdominal segment.

Growth and form are not the only metabolic processes in *Artemia* influenced by the genetic constitution of the animal : physiological differences occur between animals from different localities. The oxygen consumption of parthenogenetic females from southern France, when measured under standard conditions, is higher than that of females derived from the bisexual Californian stock (Gilchrist, 1959). The higher metabolic activity of the parthenogenetic females is also reflected in their growth rate (Fig. 1). It seems, therefore, that local geographical races of *Artemia* should be recognised, each with their particular morphological and physiological characteristics. These are a property of the animals themselves, irrespective of the salinity of the external medium. In consequence of this the influence of external environmental factors on the metabolic activities of *Artemia* should be considered in relation to the modifying effects of intrinsic factors.

ACKNOWLEDGMENTS

It is a pleasure to thank Professor H. Munro Fox, F.R.S. for much helpful discussion during the course of this work. Dr J. Green has kindly read and criticised the manuscript. Part of this work was aided by a grant from the Central Research Fund of the University of London.

REFERENCES

Abonyi, A. (1915). Experimentelle Daten zum Erkennen der *Artemia* Gattung. *Z. wiss. Zool.* **114** : 95–168.

ALLEN, E. J. & NELSON, E. W. (1910). On the artificial culture of marine plankton organisms. *J. Mar. biol. Ass. U.K.* **8** : 421–474.

ANIKIN, W. P. (1898). Einige biologische Beobachtungen über die Crustaceen der Gattung *Artemia*. *Zool Zbl.* **6** : 757–760.

ARTOM, C. (1907 a). La variazione dell'*Artemia salina* (Linn.) di Cagliari sotto l'influsso della salsedina. *Mem. R. Accad. Torino* **57** : 221–254.

ARTOM, C. (1907 b). Ricerche sperimentali sulla variazione dell'*Artemia salina* Lin. di Cagliari. *Biologica, Torino* **1** : 247-264.

ARTOM, C. (1931). L'origine e l'evoluzione della partenogenesi attraverso i differenti biotipi di una specie collettiva (*Artemia salina* L.) con speciale riferimento al biotipo diploide partenogenetico di Sète. *Mem. R. Accad. Ital.* **2** : 1–57.

BAID, I. C. (1959). Occurrence of neoteny in the genus *Artemia*. *Nature, Lond.* **184** : 73–75.

BARIGOZZI, C. (1939). La biologia di *Artemia salina* Leach studiata un aquario. *Atti Soc. ital. Sci. nat.* **78** : 137–160.

BARIGOZZI, C. (1957). Différenciation des génotypes et distribution géographique d'*Artemia salina* Leach : données et problèmes.

BATESON, W. (1894). *Materials for the study of variation*. London : Macmillan.

BOND, R. M. (1933). Observations on *Artemia* '*franciscana*' Kellogg, especially on the relation of environment to morphology. *Int. Rev. Hydrobiol.* **28** : 117–125.

BUTCHER, R. W. (1959). An introductory account of the smaller algae of British coastal waters. Part 1. Introduction and Chlorophyceae. *Fish. Invest.* **4** : 1-74.

DADAY DE DEÉS, E. (1910). Monographie systématique des Phyllopodes Anostracés. *Ann. Sci. nat. Zool.* (9) **11** : 91–489.

ELIASSEN, E. (1952). The energy metabolism of *Artemia salina* in relation to body size, seasonal rhythms and different salinities. *Univ. Bergen Årb. naturv. R.* **11** : 1–18.

FOX, H. M., GILCHRIST, B. M. & PHEAR, E. A. (1951). Functions of haemoglobin in *Daphnia*. *Proc. Roy. Soc.* (B) **138** : 514-528.

GILCHRIST, B. M. (1954). Haemoglobin in *Artemia*. *Proc. Roy. Soc.* (B) **143** : 136–146.

GILCHRIST, B. M. (1956). The oxygen consumption of *Artemia salina* (L.) in different salinities. *Hydrobiologia* **8** : 54–65.

GILCHRIST, B. M. (1959). The metabolism of *Artemia salina* (L.). Ph.D. thesis : University of London.

GOLDSCHMIDT, E. (1952). Fluctuations in chromosome number in *Artemia salina*. *J. Morph.* **91** : 111–131.

GROSS, F. (1932). Untersuchungen über die Polyploidie und die Variabilität bei *Artemia salina*. *Naturwissenschaften* **20** : 962–967.

HARVEY, H. W. (1955). *The chemistry and fertility of sea waters*. Cambridge : University Press.

HEATH, H. (1924). The external development of certain phyllopods. *J. Morph.* **38** : 453–483.

JENSEN, A. C. (1918). Some observations on *Artemia gracilis*, the brine shrimp of Great Salt Lake. *Biol. Bull., Woods Hole* **34** : 18–25.

KELLOGG, V. L. (1906). A new *Artemia* and its life conditions. *Science, N.Y.* **24** : 594–596.

KUENEN, D. J. (1939). Systematical and physiological notes on the brine shrimp, *Artemia*. *Arch. néerl. Zool.* **3** : 365–449.

LINDER, F. (1941). Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. *Zool. Bidr. Uppsala* **20** : 103–302.

LOCHHEAD, J. H. & LOCHHEAD, M. S. (1941). Studies on the blood and related tissues in *Artemia* (Crustacea Anostraca). *J. Morph.* **68** : 593–632.

MARTIN, E. G. & WILBUR, B. C. (1921). Salt antagonism in *Artemia*. *Amer. J. Physiol.* **55** : 290–291.

SAMTER, M. & HEYMONS, R. (1902). Die Variationen bei *Artemia salina* Leach, und ihre Abhängigkeit von äusseren Einflüssen. *Abh. preuss. Akad. Wiss.* **2** : 1–62.

SCHMANKEWITSCH, W. J. (1875). Ueber das Verhältniss der *Artemia salina* Miln. Edw. zur *Artemia Muhlhausenii* Miln. Edw. und dem Genus *Branchipus* Schaeff. *Z. wiss. Zool.* Suppl. **25** : 103–116.

SCHMANKEWITSCH, W. J. (1877). Zur Kenntniss der Einflusses der äusseren Lebensbedingungen auf die Organisation der Thiere. *Z. wiss. Zool.* **29** : 429–494.

STELLA, E. (1933). Phaenotipical characteristics and geographical distribution of several biotypes of *Artemia salina* L. *Z. indukt. Abstamm.- u. VererbLehre* **65** : 412–446.

THOMPSON, d'A. W. (1942). *On growth and form.* Cambridge : University Press.

WARREN, H. S. (1938). The segmental excretory glands of *Artemia salina* Linn., var. principalis Simon (the brine shrimp). *J. Morph.* **62** : 263–289.

WEISZ, P. B. (1946). The space time pattern of segment formation in *Artemia salina*. *Biol. Bull., Woods Hole* **91** : 119–140.

FURTHER NOTES ON THE GENUS *PHANEROPTERA* SERVILLE, WITH A REVISED KEY TO THE SPECIES (ORTHOPTERA: TETTIGONIIDAE)

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[Accepted 9th February 1960]

(With 56 figures in the text)

This paper is a second supplement to the author's revision of *Phaneroptera* Serville (Ragge, 1956). Further notes are given on several of the species, and a new species from East Africa is described. A completely revised key to the species is also included.

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INTRODUCTION

Since the author's revision of *Phaneroptera* Serville (Ragge, 1956) and a later supplementary paper (Ragge, 1957), further interesting facts, including a new species, have become evident, and it seems worth putting this new information on record.

In the description of the new species the wing-vein nomenclature used is that of Ragge (1955) and the author's usual conventions are observed (see Ragge, 1957, p. 124).

I am much indebted to Professor G. Ya. Bei-Bienko and Dr L. Mistshenko of the U.S.S.R. Academy of Sciences, Leningrad, for sending me specimens of *Phaneroptera cretacea* Uvarov, *Ph. bivittata* Bei-Bienko, and *Ph. spinosa* Bei-Bienko. I wish also to thank Miss P. M. Stock for help with the measurements of *Ph. fragilis* sp. n.

REVISED KEY TO THE SPECIES

The key to males is substantially the same as that of Ragge (1956), with the addition of *Ph. cretacea* Uvarov, *Ph. trigonia* Ragge, and *Ph. fragilis* sp. n. The male sex of *Ph. longicauda* (Willemse) is still unknown.

Ph. cretacea Uvarov, *Ph. longispina* Ragge, and *Ph. trigonia* Ragge, have been added to the key to females, and I have attempted to improve the means of identifying members of this sex in some of the more difficult species. It must be strongly emphasized, however, that it is often very difficult and sometimes impossible to identify the species in the absence of the male sex,

and identifications of all but the first seven species mentioned made with the key to females should be regarded as very tentative. The female sex is unknown in *Ph. maculosa* Ragge and *Ph. fragilis* sp. n.

MALES

1. Hind tibiae with two apical spurs on each side, as in Fig. 2..	*Ph. albida* Walker.
—. Hind tibiae with three apical spurs on each side, as in Fig. 1..	2.
2. Tenth abdominal tergite much enlarged, as in Figs. 3 or 4, forming a hood over the supra-anal plate, which is not bifurcate and usually hidden.....	3.
—. Tenth abdominal tergite not as in Figs. 3 or 4, unmodified, or, if slightly enlarged (*Ph. furcifera* Stal), supra-anal plate deeply bifurcate (Fig. 5). Supra-anal plate always visible	4.
3. Posterior margin of the tenth abdominal tergite smoothly rounded (Fig. 3). Cerci with a conspicuous bulge towards the distal end, which is not spatulate (Fig. 9). Subgenital plate as in Fig. 18.....	*Ph. brevis* (Serville).
—. Posterior margin of the tenth abdominal tergite with an acute median projection (Fig. 4). Cerci without a bulge, spatulate apically (Fig. 10). Subgenital plate as in Fig. 19	*Ph. celebica* Haan.
4. Cerci with a large, blunt, dorsal tooth about halfway along their length	*Ph. dentata* (Willemse).
—. Cerci without a dorsal tooth halfway along their length....	5.
5. Dorsal spines of the hind tibiae large and widely spaced, as in Fig. 24.....	*Ph. longispina* Ragge.
—. Dorsal spines of the hind tibiae small and closely spaced, as in Figs. 22 and 23.....	6.
6. Subgenital plate deeply bifurcate, as in Figs. 25 and 26	7.
—. Subgenital plate not as in Figs. 25 and 26	8.
7. Stridulatory organ broad, as in Fig. 31. Fore coxal spine very small or absent.....	*Ph. acaciae* Chopard.
—. Stridulatory organ narrower, as in Fig. 30. Fore coxal spine well-developed	*Ph. fragilis* sp. n.
8. Costal and precostal areas of the fore wings more or less translucent or whitish, with a sparser venation than the remaining areas	9.
—. Costal and precostal areas of the fore wings of the same texture as the remaining areas and not whitish.....	11.
9. Lateral pronotal lobes with a ventral white band. Cerci undulate distally, as in Fig. 11.....	*Ph. cretacea* Uvarov.
—. Lateral pronotal lobes without a ventral white band. Cerci not undulate distally, as in Figs. 12 and 13.....	10.
10. Fore wings more than 17 mm. in length. Hind femora attenuate, as in Fig. 33. Cerci as in Fig. 12.....	*Ph. gracilis* Burmeister (marginate form).
—. Fore wings less than 17 mm. in length. Hind femora not attenuate, as in Fig. 34. Cerci as in Fig. 13.....	*Ph. minima* Brunner.*
11. Fore wings less than 13 mm. in length. Hind wings extending beyond the fore wings by at least two-thirds of the length of the latter.....	*Ph. parva* Ragge.

* Specimens of *Ph. nana sparsa* Stal with "arid" facies would run out here (see p. 247); *Ph. minima* Brunner may be distinguished from them by the coloration of the fore wings (see Ragge, 1956, p. 248).

—. Fore wings more than 13 mm. in length. Hind wings extending beyond the fore wings by less than two-thirds of the length of the latter ..... 12.

12. Distal part of the cerci bent vertically, with the apex directed upwards, as in Figs. 35 and 36 ..... 13.

—. Cerci not as in Figs. 35 and 36, curved only in the horizontal plane, with the apex not directed upwards ..... 14.

13. Cerci as in Fig. 35. Supra-anal plate wider than long, as in Fig. 6. Subgenital plate very broad with spreading lobes, as in Fig. 28 ..... *Ph. falcata* (Poda).

—. Cerci as in Fig. 36. Supra-anal plate quadrate, as in Fig. 7. Subgenital plate comparatively slender with almost contiguous lobes, as in Fig. 27 ..... *Ph. myllocerca* Ragge.

14. Cerci as in Figs. 54–56. Hind femora usually attenuate, as in Fig. 33, but are not so in specimens from the northernmost parts of the range in Asia (see p. 249) ..... *Ph. gracilis* Burmeister.

—. Cerci not as in Figs. 54–56. Hind femora not attenuate, as in Fig. 34 ..... 15.

15. Subgenital plate considerably thickened and sharply truncate at the apex, as in Fig. 20. Tenth abdominal tergite somewhat enlarged ..... *Ph. furcifera* Stal.

—. Subgenital plate relatively thin, bilobate at the apex. Tenth abdominal tergite unmodified ..... 16.

16. Distal lobes of the subgenital plate smoothly rounded, as in Figs. 21 and 23 ..... 17.

—. Distal lobes of the subgenital plate not as in Figs. 21 and 23, more or less pointed ..... 18.

17. Cerci as in Fig. 14 ..... *Ph. neglecta* (Karny).

—. Cerci as in Fig. 15 ..... *Ph. trigonia* Ragge.

18. Apex of the cerci abruptly bent inwards, as in Fig. 16 ..... *Ph. curvata* (Willemse).

—. Cerci not as in Fig. 16 ..... 19.

19. Stridulatory organ large, almost as wide as long, as in Fig. 32 *Ph. nigroantennata* Brunner.

—. Stridulatory organ relatively smaller, not shaped as in Fig. 32 20.

20. Fore wings with dark brown cells and green veinlets (Formosa) *Ph. trigonia* Ragge.

—. Fore wings not coloured as above (Europe and Africa) ..... 21.

21. Hind femora more than 19 mm. in length ..... *Ph. magna* Ragge.

—. Hind femora less than 19 mm. in length ..... 22.

22. Vertex very convex with steeply sloping fastigium, as in Fig. 37. Colour mottled brown and black ..... *Ph. maculosa* Ragge.

—. Vertex only slightly convex with almost horizontal fastigium, as in Fig. 38. Colour green (rarely brown) ..... 23.

23. Antennae variegated with pale and dark bands. Hind tibiae with less than 35 external dorsal spines ..... *Ph. nigropunctata* Chopard.

—. Antennae unicolorous (rarely with narrow pale bands). Hind tibiae usually with more than 35 external dorsal spines. *Ph. nana* Fieber.

FEMALES

1. Hind tibiae with two apical spurs on each side, as in Fig. 2 .. *Ph. albida* Walker

—. Hind tibiae with three apical spurs on each side, as in Fig. 1 .. 2.

2. Ovipositor more than 7 mm. in length, shaped as in Fig. 42 .. *Ph. longicauda* (Willemse).

—. Ovipositor less than 7 mm. in length, or, if more than 7 mm., not shaped as in Fig. 42 ..... 3.

3. Costal and precostal areas of the fore wings more or less translucent or whitish, with a sparser venation than the remaining areas ..... 4.

—.	Costal and precostal areas of the fore wings of the same texture as the remaining areas and not whitish	7.
4.	Lateral pronotal lobes with a ventral white band	*Ph. cretacea* Uvarov.
—.	Lateral pronotal lobes without a ventral white band	5.
5.	Ovipositor shaped as in Fig. 40. Fore wings brown	*Ph. acaciae* Chopard.
—.	Ovipositor not shaped as in Fig. 40. Fore wings not brown	6.
6.	Hind femora attenuate, as in Fig. 33. Lateral pronotal lobes shaped as in Fig. 44. Fore wings usually more than 20 mm. in length	*Ph. gracilis* Burmeister (marginate form).
—.	Hind femora not attenuate, as in Fig. 34. Lateral pronotal lobes shaped as in Fig. 43. Fore wings usually less than 20 mm. in length	*Ph. minima* Brunner.*
7.	Dorsal spines of the hind tibiae large and widely spaced, as in Fig. 24	*Ph. longispina* Ragge.
—.	Dorsal spines of the hind tibiae small and closely spaced, as in Figs. 22 and 23	8.
8.	Fore wings less than 15 mm. in length. Hind wings extending beyond the fore wings by at least two-thirds of the length of the latter	*Ph. parva* Ragge.
—.	Fore wings more than 15 mm. in length. Hind wings extending beyond the fore wings by less than two-thirds of the length of the latter	9.
9.	European, Asiatic, and African species	10.
—.	Austro-Malayan species	22.
10.	European species	11.
—.	Asiatic and African species	12.
11.	Lateral pronotal lobes deeper than long, as in Fig. 45	*Ph. nana* Fieber.
—.	Lateral pronotal lobes about as long as deep, as in Fig. 48	*Ph. falcata* (Poda).
12.	African species	13.
—.	Asiatic species	16.
13.	Hind femora attenuate, as in Fig. 33. Lateral pronotal lobes longer than deep, as in Fig. 44	*Ph. gracilis* Burmeister.
—.	Hind femora not attenuate, as in Fig. 34. Lateral pronotal lobes at least as deep as long, not as in Fig. 44	14.
14.	Ovipositor more than 6 mm. in length, shaped as in Fig. 41	*Ph. magna* Ragge.
—.	Ovipositor less than 6 mm. in length, shaped as in Fig. 39	15.
15.	Antennae variegated with pale and dark bands Hind tibiae with less than 35 external dorsal spines	*Ph. nigropunctata* Chopard
—.	Antennae unicolorous (rarely with narrow pale bands). Hind tibiae usually with more than 35 external dorsal spines	*Ph. nana* Fieber.
16.	Fore wings with a dark brown or red-brown band along the posterior margin	17.
—.	Fore wings unicolorous	19.
17.	Lateral pronotal lobes longer than deep, as in Fig. 44	*Ph. gracilis* Burmeister.
—.	Lateral pronotal lobes at least as deep as long, as in Figs. 46 and 47	18.
18.	Fore wings with dark brown cells and green veinlets (Japan and Formosa)	*Ph. nigroantennata* Brunner.
—.	Fore wings uniformly green, except for posterior margin (India, Kashmir, Sikkim, Burma, and China)	*Ph. myllocerca* Ragge.
19.	Antennae dark brown except near base	20.
—.	Antennae pale coloured	21.
20.	Maximum vertical width of the hind femora more than 2 mm.	*Ph. trigonia* Ragge.
—.	Maximum vertical width of the hind femora less than 2 mm.	*Ph. gracilis* Burmeister.

*See footnote on p. 238.

21. Lateral pronotal lobes longer than deep, as in Fig. 44..... *Ph. gracilis* Burmeister.
—. Lateral pronotal lobes about as deep as long, as in Fig. 48.... *Ph. falcata* (Poda).
22. Ovipositor with a protruding flap at the base of the dorsal margin of the lower valves, beneath each basal lobe, as in Fig. 50 ..... *Ph. curvata* (Willemse).
—. Ovipositor without protruding flaps, as in Fig. 49..... 23.
23. Base of the anal area of the fore wings conspicuously darkened ..... *Ph. celebica* Haan.
—. Base of the anal area of the fore wings not darkened..... 24.
24. Tenth abdominal tergite slightly produced posteriorly, as in Fig. 51 ..... *Ph. brevis* Serville.
—. Tenth abdominal tergite unmodified, as in Fig. 52..... 25.
25. Hind femora attenuate, as in Fig. 33. Fore wings usually more than 20 mm. in length..... *Ph. gracilis* Burmeister.
—. Hind femora not attenuate, as in Fig. 34. Fore wings usually less than 20 mm. in length..... *Ph. neglecta* (Karny) and *Ph. furcifera* Stal.

(There is at present no known constant character for separating the females of these two species, but see Ragge, 1956, p. 263.)

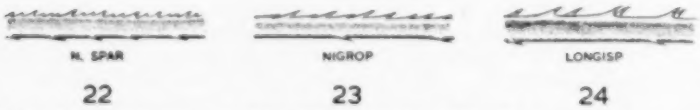
Figs. 1 & 2.—Lateral view of the apex of the left hind tibia of (1) *Phaneroptera nana* Fieber ; (2) *Ph. albida* Walker.

Figs. 3 & 4.—Lateral and dorsal views of the male tenth abdominal tergite of (3) *Phaneroptera brevis* Serville ; (4) *Ph. celebica* Haan.

Figs. 5-8.—Dorsal view of the male supra-anal plate of (5) *Phaneroptera furcifera* Stal ; (6) *Ph. falcata* (Poda) ; (7) *Ph. myllocerca* Ragge ; (8) *Ph. fragilis* sp. n.

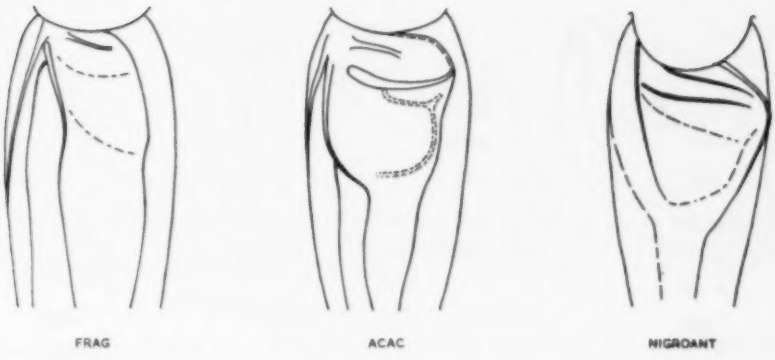
Figs. 9–17.—Dorsal view of the left male cercus of (9) *Phaneroptera brevis* Serville ; (10) *Ph. celebica* Haan ; (11) *Ph. cretacea* Uvarov ; (12) *Ph. gracilis* Burmeister ; (13) *Ph. minima* Brunner ; (14) *Ph. neglecta* (Karny) ; (15) *Ph. trigonia* Ragge ; (16) *Ph. curvata* (Willemse); (17) *Ph. fragilis* sp. n.

Figs. 18–21.—Lateral and end views of the male subgenital plate of (18) *Phaneroptera brevis* Serville ; (19) *Ph. celebica* Haan ; (20) *Ph. furcifera* Stal ; (21) *Ph. neglecta* (Karny).



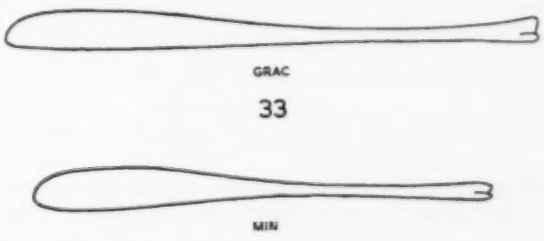
Figs. 22–24.—Lateral view of part of the left hind tibia of (22) *Phaneroptera nana sparsa* Stal ; (23) *Ph. nigropunctata* Chopard ; (24) *Ph. longispina* Ragge.

Figs. 25–29.—Ventral view of the male subgenital plate of (25) *Phaneroptera acaciae* Chopard ; (26) *Ph. fragilis* sp. n. ; (27) *Ph. myllocerca* Ragge ; (28) *Ph. falcata* (Poda) ; (29) *Ph. trigonia* Ragge.



30 31 32

Figs. 30–32.—Dorsal view of the stridulatory organ of (30) *Phaneroptera fragilis* sp. n. ; (31) *Ph. acaciae* Chopard ; (32) *Ph. nigroantennata* Brunner.

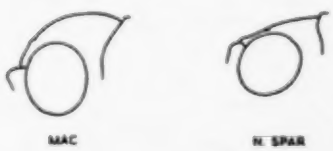


33 34

Figs. 33 & 34.—Lateral view of the left hind femur of (33) *Phaneroptera gracilis* Burmeister ; (34) *Ph. minima* Brunner.

35 36

Figs. 35 & 36.—Lateral and end views of the left male cercus of (35) *Phaneroptera falcata* (Poda) ; (36) *Ph. myllocerca* Ragge.



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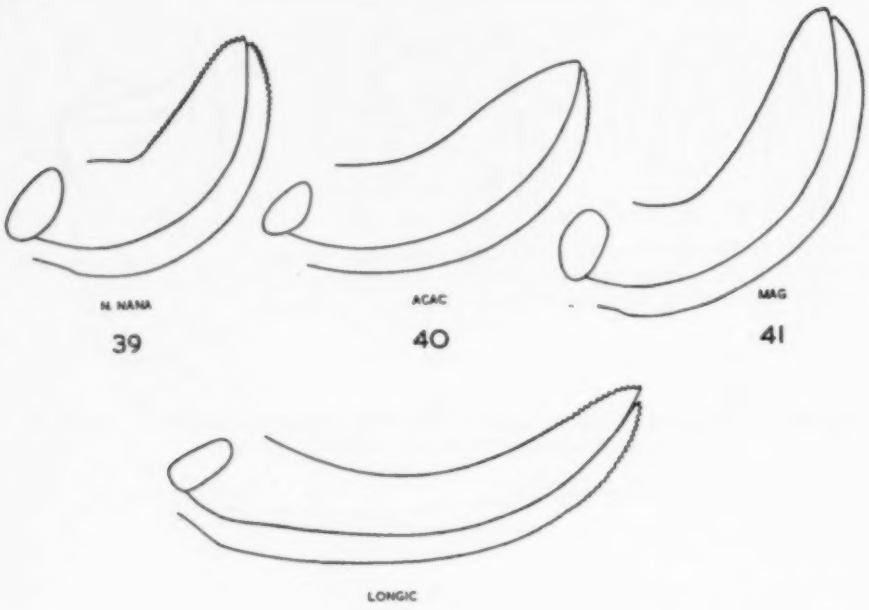
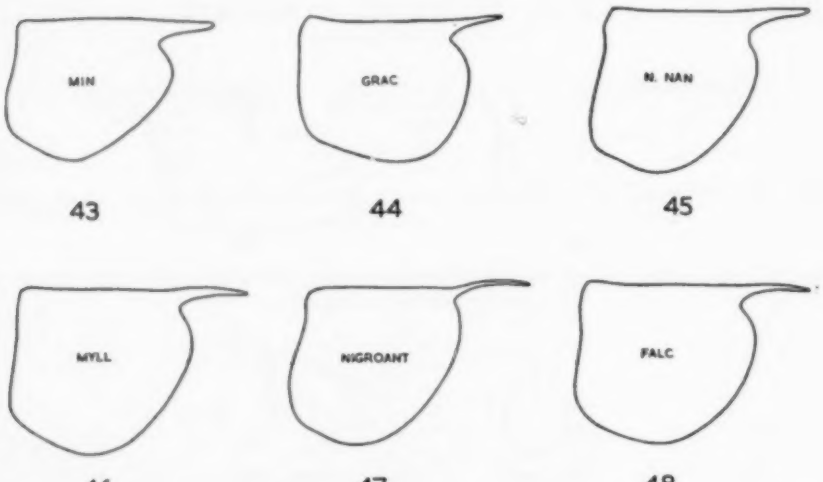
Figs. 37 & 38.—Lateral view of the dorsal part of the head of (37) *Phaneroptera maculosa* Ragge ; (38) *Ph. nana sparsa* Stal.



Figs. 39–42.—Lateral view of the ovipositor of (39) *Phaneroptera nana nana* Fieber ; (40) *Ph. acaciae* Chopard ; (41) *Ph. magna* Ragge ; (42) *Ph. longicauda* (Willemse).



Figs. 43–48.—Lateral view of the pronotum of (43) *Phaneroptera minima* Brunner ; (44) *Ph. gracilis* Burmeister ; (45) *Ph. nana nana* Fieber ; (46) *Ph. myllocerca* Ragge ; (47) *Ph. nigroantennata* Brunner ; (48) *Ph. falcata* (Poda).

Figs. 49–52.—*Phaneroptera* Serville. 49 & 50.—Ventral view of the base of the ovipositor of (49) *Ph. brevis* Serville ; (50) *Ph. curvata* (Willemse). 51 & 52.—Dorsal view of the female tenth abdominal tergite of (51) *Ph. brevis* Serville ; (52) *Ph. neglecta* (Karny).

PHANEROPTERA FRAGILIS sp. n.

Holotype ♂, ETHIOPIA : Danot, 25. xi. 1953 (Popov). In the British Museum (Natural History).

Diagnosis

♂. Subgenital plate deeply bifid, as in Fig. 26. Areas C and Sc of fore wings transparent. Supra-anal plate transverse, with distinct posterior angle on each side, as in Fig. 8. Cerci as in Fig. 17, with minute subapical spine.

♀ unknown.

Description

Fastigium of vertex moderately compressed, sulcate above, hardly or not at all raised at apex.

Pronotum without lateral carinae. Spine of fore coxae well-developed. Fore tibiae with 2–3 external spurs, including 1 or 2 apical ones. Mid tibiae somewhat swollen in basal half, and with 1–5 external spurs, including 1 apical one. Hind femora unarmed, or sometimes with one very small ventral spinule near apex. Hind tibiae with about 45–65 external dorsal spines, and 3 apical spurs on each side. Venation of fore wings rather irregular ; R_s sometimes bifurcate but usually unbranched. Sc considerably swollen near its base. Areas C and Sc transparent. Bases of areas MA and Cu_{1a} of right fore wing transparent with reduced venation. Hind wings extending beyond fore wings by about half length of latter.

Tenth abdominal tergite unmodified. Supra-anal plate transverse, with distinct posterior angle on each side, as in Fig. 8. Cerci as in Fig. 17, with minute subapical spine. Subgenital plate deeply bifurcate, as in Fig. 26.

Coloration green, with red-brown spots on pronotum, parts of legs, abdominal tergites, and sometimes vertex. Tibial spines and spurs dark-tipped Cells of posterior and distal parts of fore wings brown. Hind wings hyaline except for exposed part. Cerci with dark tip.

♀ unknown.

Measurements (in millimetres)

Males

Total length (8) : 18·7–22·8, mean 20·85.
Median length of pronotum (7) : 2·2–2·4, mean 2·35.
Length of hind femur (6) : 13·0–14·2, mean 13·47.

Maximum vertical width of hind femur (6) : 1·4–1·5, mean 1·42.
Length of fore wing (8) : 10·7–13·4, mean 12·34.
Length of exposed part of hind wing (8) : 5·5–6·9, mean 6·00.

Variation

The armature of the hind tibiae is very variable. The venation of the fore wings shows much variation, especially in the branching of the radius. There may or may not be a ventral spinule near the tip of the hind femora and it is probable that there are occasionally more than one. The extent of the red-brown maculation varies somewhat.

Discussion

This species is closely allied to *Ph. acaciae* Chopard, from which it may readily be distinguished by the well-developed fore coxal spine and (in the male) by the stridulatory organ and cerci. *Ph. fragilis* sp. n. and *Ph. acaciae* Chopard are the only species of the genus in which the males have a deeply bifid subgenital plate.

Material examined

♂ holotype ; 4 ♂ paratypes, same data as holotype ; 1 ♂ paratype, Ethiopia : El Rago, 4. xii. 1953 (Popov) ; 1 ♂ paratype, British Somaliland : Haud, 8° 28′ N, 45° 38′ E, 2,500 ft., night, 23. v. 1932 (Taylor) ; 1 ♂ paratype, Ethiopia : Wardere, 7–9. xi. 1952 (Stephenson).

All in the British Museum (Natural History).

Distribution

This species is known only from a small area in the vicinity of the border between Ethiopia and British Somaliland, but it doubtless occurs over a much larger part of this semi-desert area of eastern Africa.

PHANEROPTERA CRETACEA Uvarov, 1929

Phaneroptera cretacea Uvarov, 1929, *Annu. Mus. zool. Acad. St. Pétersb.* **30** : 629.

Holotype ♂, S.E. Persia : Bampur and environs, 12. iv. 1901 (Zarudny). In the Zoological Museum of the U.S.S.R. Academy of Sciences, Leningrad.

Dr L. Mistshenko has very kindly lent me the male holotype of this interesting species, together with a female specimen (from Fars, in southern Persia). As I suggested in my revision of 1956, there is a very close resemblance in colour between this species and *Ph. albida* Walker. *Ph. cretacea* Uvarov, however, has six apical spurs on each hind tibia instead of the four shown by *Ph. albida* Walker, and thus both sexes of the two species may be easily separated.

The fastigium of the frons is broader and much blunter apically in the holotype of this species than is usual in *Phaneroptera* Serville. However, the female specimen was rather more normal in this respect, and this feature may be subject to variation. The male cerci (Fig. 11) differ clearly from those of *Ph. albida* Walker, and the other deserticolous species *Ph. minima* Brunner, in being undulate towards the apex, which is blunt.

PHANEROPTERA BIVITTATA Bei-Bienko, 1954

Phaneroptera bivittata Bei-Bienko, 1954, Fauna of the U.S.S.R., *Fauna Rossii* (New Series) Orthoptera **2** (2) : 74.

Holotype ♂, ARMENIA : Dhuga, nr. Dzhulfa, on R. Araks, 4. vii. 1931 (Riabov). In the Zoological Museum of the U.S.S.R. Academy of Sciences, Leningrad.

Since my 1956 revision Professor Bei-Bienko has very kindly presented the British Museum (Natural History) with a paratype of this species (from the type locality), and I am thus able to make further remarks about it.

I suggested in 1956 (p. 238) that *Ph. bivittata* Bei-Bienko might represent a further subspecies of *Ph. nana* Fieber or perhaps a north-eastern form of *Ph. n. sparsa* Stal. This interesting possibility seems to be well substantiated by an examination of the paratype. This specimen has certain features, especially in its coloration, which seem at first sight to separate it fairly clearly from *Ph. nana* Fieber. There is a white band along each side of the pronotal disc ; the black spots typically found on the stridulatory organ in *Ph. nana* Fieber are lacking ; the posterior margin of the fore wings (area Cu_{1a}) is noticeably translucent and whitish in colour ; and there is a conspicuous whitening of much of the ventral and lateral parts of the body. None of these features is found in typical specimens of either of the two subspecies of *Ph. nana* Fieber. However, a further examination of the British Museum collection of *Ph. n. sparsa* Stal showed that a marked tendency towards this type of coloration occurs whenever this subspecies is found in unusually arid conditions. Some specimens from Ethiopia, British Somaliland, northern Kenya, the more arid parts of Tanganyika, parts of the Arabian peninsular, the fringes of the Syrian Desert, and a recently acquired specimen from Afghanistan, all show some or all of these features in their coloration. A few of the specimens are almost indistinguishable from the paratype of *Ph. bivittata* Bei-Bienko ; this is especially true of certain specimens from the drier parts of Israel (kindly sent to me by Dr M. P. Pener of the Hebrew University, Jerusalem), where the vegetation and climate have much in common with the steppe country of Armenia and Kopet Dagh (the two localities from which the original material of *Ph. bivittata* Bei-Bienko was collected). The fore wing-length/hind femur-length ratio in these Israeli specimens with " arid " facies is usually 1·1. This value, which is also shown by the specimen from Afghanistan, is high for *Ph. n. sparsa* Stal, as would be expected in specimens from the northernmost parts of the range. The measurements given by Bei-Bienko for *Ph. bivittata* Bei-Bienko also suggest a mean ratio of about 1·1, though the paratype presented to the British Museum has the lower value of 1·0.

It seems clear from these observations that the range of *Ph. n. sparsa* Stal (Fig. 53) crosses the Anatolian Steppe to Armenia and extends eastwards along a narrow strip of high steppe between the Kara Kum Desert and the Iranian Plateau to the mountains of Hindu Kush. This suggests that the distribution was very much more widespread in quite recent times but has since become greatly restricted by the development of vast areas of desert and dry steppe in south-west Asia.

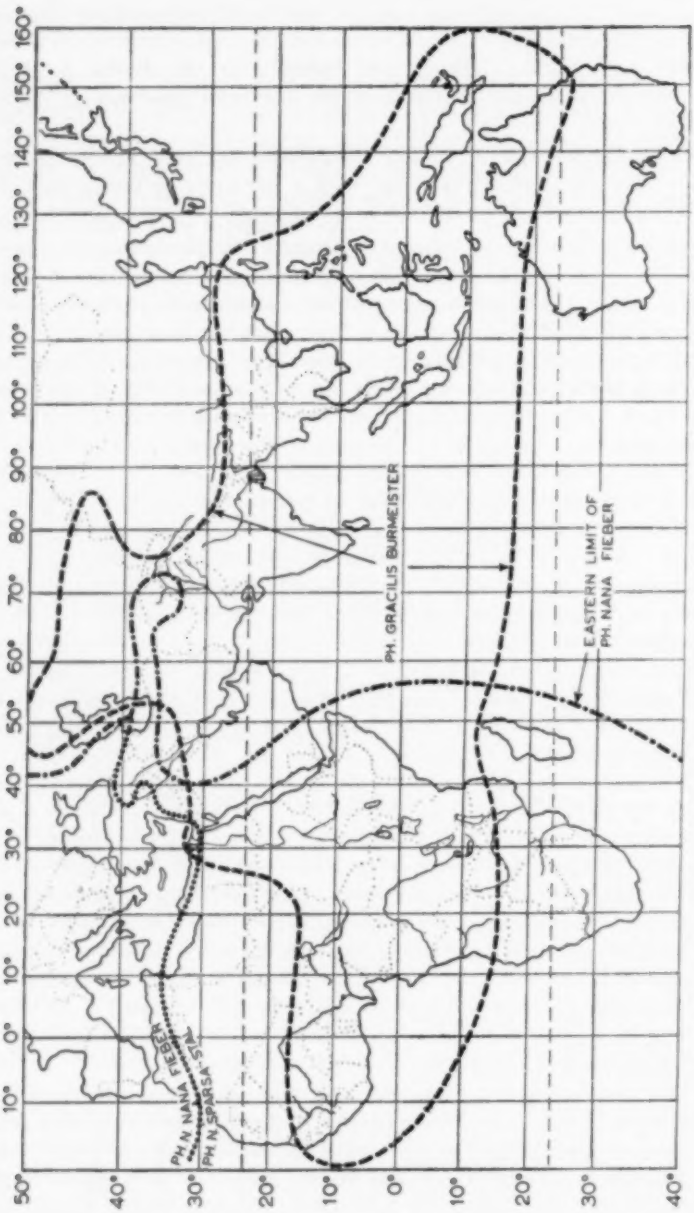


Fig. 53.—Map showing the approximate distributions of *Phaneroptera nana* Fieber and *Ph. gracilis* Burmeister.

As the distinctive features shown by this north-eastern form of *Ph. n. sparsa* Stal arise whenever the subspecies encounters unusually arid conditions, it would clearly be unwise to regard it as a distinct subspecies. The name *bivittata* Bei-Bienko can be usefully applied at the varietal level, however, to the specimens of *Ph. n. sparsa* Stal which show " arid " facies.

PHANEROPTERA SPINOSA Bei-Bienko, 1954

Phaneroptera spinosa Bei-Bienko, 1954, Fauna of the U.S.S.R., *Fauna Rossii* (New Series), Orthoptera **2** (2) : 75.

Holotype ♂, KAZAKHSTAN : Karzhantau Mtns., N.E. of Tashkent, Ak-Tash, 29. viii. 1937 (Obukhova). In the Zoological Museum of the U.S.S.R. Academy of Sciences, Leningrad.

This species was not included in my revision of 1956 as I was unable to draw any conclusions as to its status from the original description. However, Professor Bei-Bienko has now kindly presented the British Museum with a paratype of each sex from near the type locality (Talasskij Alatau, R. Ak-Su, nr. Novonikolaevka, 15. xi. 1935), and some interesting facts have emerged.

Ph. spinosa Bei-Bienko resembles *Ph. gracilis* Burmeister in its rather elongate appearance and in the general nature of the male genitalia, but the hind femora differ in not being attenuate, and the male cerci show a difference in the shape of the apex. The degree of attenuation of the hind femora, however, shows considerable geographical variation in *Ph. gracilis* Burmeister and specimens from the northernmost parts of the range are not markedly different in this character from *Ph. spinosa* Bei-Bienko. The male cerci also vary geographically, and at 7,000–8,000 ft. on the lower slopes of the Himalayas (e.g. Mussoorie and Muktesar) a form appears which has male cerci of the same type as *Ph. spinosa* Bei-Bienko, perhaps carrying the modification to an even greater extreme (see Figs. 54–56). The difference in outline shown by Figs. 55 and 56, as compared with the normal type (Fig. 54), is accompanied by an appreciable dorso-ventral flattening, giving the cercus a rather spade-like appearance towards the apex. The hind femora of this Himalayan form are more attenuate than in *Ph. spinosa* Bei-Bienko and do not differ in shape from those of more typical specimens of *Ph. gracilis* Burmeister coming from the neighbouring lowlands of northern India.

54 55 56

Figs. 54–56.—Dorsal view of the left cercus of male specimens of *Phaneroptera gracilis* Burmeister from (54) southern India ; (55) Kazakhstan (paratype of *Ph. spinosa* Bei-Bienko) ; (56) Himalayas.

The known range of *Ph. gracilis* Burmeister at the time of my revision (Ragge, 1956, Fig. 101) was already quite remarkable, covering most of the Old World between the latitudes of 30° N and 20° S. Arabia has since been included on the basis of a specimen of each sex from Riyadh (xi. 1937 and 12. ix. 1958). The fact that this species can tolerate such enormously different climates and types of vegetation, ranging from tropical rain forest to semi-desert, makes it quite feasible for its range to extend into the arid areas of south-west Asia, where the climate has much in common with that of Egypt and Arabia. It seems that *Ph. spinosa* Bei-Bienko and the Himalayan specimens represent a northern form of *Ph. gracilis* Burmeister, and the known range of this species thus becomes even more remarkable (Fig. 53) ; it is quite probable that Persia, Afghanistan, and perhaps even parts of Mongolia may eventually be included. Whether it is practicable to regard the northern form as a distinct subspecies can be decided only when more material becomes available, so that it can be seen whether the change in the shape of the cerci is a gradual or abrupt one. The subspecies would have to take the name *Ph. g. indica* Brunner, 1878, as a re-examination of the two syntypes (1 ♂ and 1 ♀) of *Ph. indica* Brunner (through the kindness of Dr M. Beier) has shown that the male has cerci of this northern type (Fig. 56) ; I have selected and marked this specimen as a lectotype.

REFERENCES

RAGGE, D. R. (1955). *The wing-venation of the Orthoptera Saltatoria.* London : British Museum (Natural History).

RAGGE, D. R. (1956). A revision of the genera *Phaneroptera* Serville and *Nephoptera* Uvarov (Orthoptera : Tettigoniidae), with conclusions of zoogeographical and evolutionary interest. *Proc. zool. Soc. Lond.* **127** : 205–283.

RAGGE, D. R. (1957). A new species of *Phaneroptera* Serville from Formosa (Orthoptera : Tettigoniidae). *Proc. R. ent. Soc. Lond.* (B) **26** : 123–126.

THE BREEDING OF SOME LARGER MAMMALS IN NORTHERN RHODESIA

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(With 11 figures in the text)

Details are given of a standard manner of recording breeding data of large mammals by game department officers, which is considered a great improvement on previous casual reporting. Information on the breeding in Northern Rhodesia of several ungulates and large Carnivora is summarised, and comparisons made with published data from other territories. It is stressed that much more study is needed, but certain points emerge from consideration of present information. Many species have their young at any time of year, and only a few have a really sharply defined birth season. The wart hog (*Phacochoerus aethiopicus*) seems markedly seasonal in the south of its range, but not in the northern parts. There is at present no data on the fluctuations in frequency of births among non-seasonal breeders. In the seasonally breeding species the actual birth months vary somewhat from north to south, and in the wildebeest (*Connochaetes taurinus*) there may be variation in the calving time due apparently to purely local differences of environment. The wild dog (*Lycaon pictus*) appears to be monoestrus, but data on the larger felids, though incomplete, seems to indicate that young may be born at any time of the year. Limiting factors in the study of breeding in African large mammals are pointed out, but it is suggested that further work on the lines of that carried out in Northern Rhodesia would be profitable.

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INTRODUCTION

Our knowledge of the breeding biology of African wild mammals is very incomplete, even among the better known species, while virtually nothing is known of many others. In the records of the Northern Rhodesia Game &

Fisheries Department a fair amount of information has been accummulated, and this has been available to me in addition to my own notes. Several game animals have, however, had to be omitted due to lack of sufficient data.

I am indebted to Messrs R. I. G. Attwell, B. L. Mitchell and J. C. Uys of my department, who have supplied much further information, and to Mr G. Hellam of the Livingstone Game Park, for useful records of births there, as well as notes on breeding of some species in the wild state.

SOURCES OF DATA

Information has been drawn largely from unpublished records of the Game & Fisheries Department, which are quoted as "dep.rec". Game reports, which were introduced in 1957 with the object of enabling officers to record data from field observations in a standard and concise manner, have been particularly useful. These reports are made on printed forms (see Appendix) and filed under individual species. One line is allotted to "Number of juveniles definitely under one month old" and from this it has been possible to obtain many more definite records of births than previously available. The advantage of such data from several different parts of the country is obvious, even though there is inevitably a subjective element in that observers may differ somewhat in their assessment of the ages of young animals seen. However, it has been particularly stressed that accuracy is of prime importance, and that in cases of doubt records of "under one month" should not be made. In the following I have guarded as far as possible against the inclusion of possibly unreliable data.

Additional notes may be included on the report forms, e.g. when a young animal still wet from birth is found, or "not under one month, but definitely under two months", this latter being useful for species which hide their newly born young for a time, and of which there are consequently few or no "under one month" reports.

I have back-dated the records to arrive as nearly as possible at the actual birth months, having regard for all relevant factors, and though it may be objected that an additional subjective element is thereby introduced it is considered that these "calculated" times of birth are as accurate as can be obtained, and they are in any case an advance on previously available data.

One thing, however, must be pointed out in connection with the records compiled as above, which, unless guarded against, might introduce serious bias. This is that most game reports are made in the dry season, from about April to October or November. This is because game is widely dispersed during the remainder of the year, and opportunity for observation is further limited by the tall grass, while routine patrolling by game staff is at a minimum during the rains. The main result of the scarcity of wet season reports is to leave gaps in the information on species believed to have young throughout the year. With those markedly seasonal it may not matter, because numerous observations of the herds without young prior to the appearance of the first calves of the year may leave no doubt as to the periodic nature of their breeding.

Records of births of certain species in the Livingstone Game Park have been made available by Mr G. Hellam. This Game Park is not a National

Park in the accepted sense, with animals in the wild state, but an enclosed area of about 1000 acres into which local ungulates are imported and kept as a local attraction. Several animals have bred therein, and it is assumed that for the most part they would do so about the same time as in the wild. Livingstone Park records are quoted therefore only where particularly necessary, no special mention being made where they completely accord with observations in other parts of the territory. Births in the London Zoological Gardens have been summarised by Zuckerman (1953), and I have in some instances referred to this. But it seems advisable to exercise caution in applying data from captive animals to wild ones. In London the animals are, of course, more closely confined than in Livingstone Game Park, and in a quite different and more artificial environment.

In addition to records from Northern Rhodesia I have noted information from certain other territories, principally from published works, especially Shortridge (1934, including his quotations from other authors), Stevenson-Hamilton (1947), Verheyen (1951), Verschuren (1958), and Roosevelt & Heller (1922). Comparisons have been made where possible between these different areas in respect of the seasonally breeding species.

TEXT FIGURES

For some species I have shown recorded births in Northern Rhodesia, up to and including 1958, as histograms, and where there is marked periodicity I have given charts which show the seasons in Northern Rhodesia in comparison with other territories. In these charts peak periods are shown where possible as solid rectangles, and other months cross-hatched, but this has not been possible in all cases due to lack of sufficient data. Out-of-season births are indicated by crosses. It should be remembered that the extent and validity of the information available may vary, and the older records may often be based on general impressions and isolated cases rather than extensive detailed observations.

TERMS USED

From the literature it is obvious that the term " breeding season " is used in two different senses. It may indicate the time when the young are born, or may stand for the time of mating. To avoid ambiguity it seems best to drop the expression " breeding season " in either particular sense, and to use " season of birth " for the time the young are born (with " calving ", " lambing ", " foaling ", " farrowing " or " whelping " for special groups if desired), and " mating season " or " rut " for the other time. Such usage can cause no possible confusion.

In Northern Rhodesia certain differences in the birth times among the seasonal breeders have been found between the Luangwa Valley and the middle Zambesi Valley (below Victora Falls to Feira) on one hand and the northwestern and western plateau areas on the other. The latter are herein termed the " northwestern plateau ", and it is from this area that most of the records come.

BREEDING RECORDS OF SPECIES

PROBOSCIDEA

Elephantidae

LOXODONTA AFRICANA Blumenbach (African Elephant)

Verheyen (1951) thought April to June was the calving time for elephant in the Upemba area, while Wilhelm (cited by Shortridge, 1934) gave October to December for the Okovango and the Caprivi. But Perry (1952), from post mortem examination of many females in Uganda, concluded that breeding might take place at any time of year, without any marked season, though perhaps somewhat more frequently in the dry period, which is about December to February in Uganda. Data from N. Rhodesia shows that small calves have been seen at practically all times of the year, definite records being absent only for February. Even allowing for the fact that in a species with such a long period of infancy individual observers are likely to differ considerably in what they consider newly born young, it seems clear that calves may be born at any time in N. Rhodesia. In the Luanga Valley, where elephants are more numerous and more frequently observed than anywhere else in the territory, there is not known to be any peak calving period in the dry season (Attwell, *in litt.*)

Various authors (e.g. Roosevelt & Heller, 1922, and Verheyen, 1951) have asserted that the newly born calf remains hidden near its birth place for a short time, until able to follow the herd. But this hardly seems borne out by a more recent account of a birth described in detail (Poppleton, 1957).

Mammae : 1 pair, pectoral.

Young per birth : 1. An instance of twins has been reported from Southern Rhodesia. (Anon. 1956).

PERISSODACTYLA

Rhinocerotidae

DICEROS BICORNIS Linn. (Black Rhinoceros)

There is little information on the breeding of this animal either from N. Rhodesia or elsewhere. Pitman (1934) records a 40 lb. foetus in May in the present Lavushi Manda Game Reserve, and may have based his suggestion of a regular calving season in June on this one instance. Very young calves have been seen in the Luangwa Valley from June to October by Attwell, who believes, however, that calving may occur throughout the year. Roosevelt & Heller (1922) record that this is so in East Africa, where the young " may be produced at any season ". Wilhelm and Vaughan-Kirby (cited by Shortridge 1934) conflict in that one thought calving occurred generally during the early rains, and the other at the end of the rains, though they were referring to different areas.

It seems that there is no defined calving time, and that the above suggestions that there is may have been made on too few data.

Mammae : 1 pair (Roosevelt & Heller, 1922), inguinal.

Young per birth : 1.

Equidae

EQUUS BURCHELLI Gray (Burchell's Zebra)

Pitman (1934) considered zebra foals were born in N. Rhodesia from July to September. Fig. 1 shows eighty-one births in the northwestern plateau up to and including 1958, and confirms that July to September is indeed the peak period, with early foals a little before and late ones a little after. There are, however, several records of out-of-season births (Fig. 2) and Uys has in

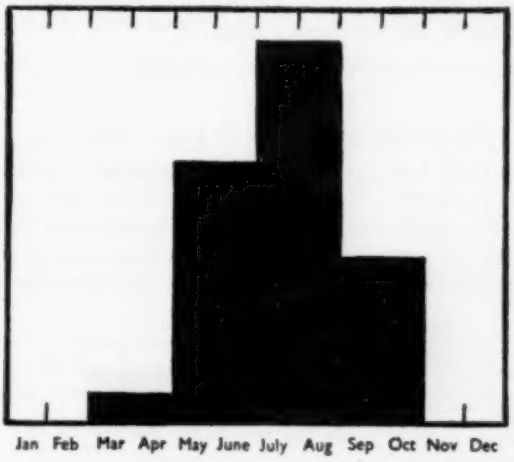

Fig. 1.—*Equus burchelli*. Eighty-one births in the Northwestern plateau areas of N. Rhodesia. From records of foals under one month old. (Combined into two-month periods to minimise possible error in calculating births).

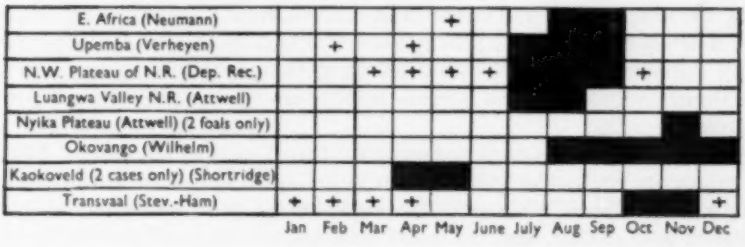
E. Africa (Neumann)
Upemba (Verheyen)
N.W. Plateau of N.R. (Dep. Rec.)
Luangwa Valley N.R. (Attwell)
Nyika Plateau (Attwell) (2 foals only)
Okovango (Wilhelm)
Kaokoveld (2 cases only) (Shortridge)
Transvaal (Stev.-Ham)
Jan Feb Mar Apr May June July Aug Sep Oct Nov Dec

Fig. 2.—*Equus burchelli*. Chart of foaling seasons in East, Central and Southern Africa.

N. Rhodesia noted that occasional young foals may be seen at any time. July to September seems to be the main foaling time in most northern parts of the speces range, but rather later in the Transvaal, and apparently more prolonged in the Okovango area. In the Luangwa Valley the foaling time corresponds with the northwestern plateau. The April and May records from the Kaoko-

veld may be isolated instances. The November record from the Nyika is of two very young foals in the same herd (Attwell, *in litt.*). 1959 records confirm the previous data for N. Rhodesia.

The newly born young have a mantle of quite long upright hairs on the back, especially over the croup, and the stripes are generally reddish brown, instead of the sepia to black seen in the adults. They run with the herd from birth.

Mammae : 1 pair, inguinal.

Young per birth : 1. (There is circumstantial evidence of an instance of twin foals in the Luangwa Valley).

ARTIODACTYLA

Suidae

POTAMOCHOERUS PORCUS Linn. (Bush Pig)

Records of recently born young from several plateau localities in N. Rhodesia are from October to March. There is one note of a litter estimated to have been born in July in Mazabuka District, but Uys, who recorded this, stated it was quite exceptional. A juvenile in captivity has been seen by C. W. Benson in Samfya District, believed to have been born in mid-September. This would

Fig. 3.—*Potamochoerus porcus.* Chart showing farrowing seasons in Central and Southern Africa.

be from an early litter. There are two instances of well developed foetuses in December, and several of sows in lactation during the rains. Other data, not formally recorded, from vermin control operations corroborate that the young are usually farrowed in the rains, as do several observations of sounders without newly born young in the dry season. Fig. 3 shows that Upemba records largely coincide with the N. Rhodesia data, though there appear to be none after December. The South African records are also similar, though perhaps incomplete.

Sows usually make a nest, or bower, for their litters in tall grass. The new born young are marked longitudinally with yellowish stripes on a brown ground, which is later followed by a reddish coat, basically as in the adults. With age the colour gets darker, and old boars may appear black all over, apart from the white dorsal crest.

Mammae : 3 pairs, lower abdominal (Sometimes there may be only 2 pairs).

Young per birth : 2–6 (usually 3 or 4 in N. Rhodesia) Verheyen suggests young sows have 3–4 in the first litter, and subsequently 5–6. The figure of 6–8 given by Asdell (1946) is too high, at least for N. Rhodesia.

PHACOCHOERUS AETHIOPICUS Pallas (Wart Hog)

Fig. 4 shows thirty births in the northwestern plateau recorded up to and including 1958, and indicates a definite peak in July and August, with early litters in June and late ones to October. 1959 figures are in agreement with the previous ones. On several occasions sounders without newly born young have been seen up to June. For example in the Northwestern Province totals of twenty-seven and twenty-eight animals were seen in two successive seasons in May–June without any of the season's new arrivals. In the Kafue National Park, Namwala sector, Uys noted " no young yet " in June 1957, and later

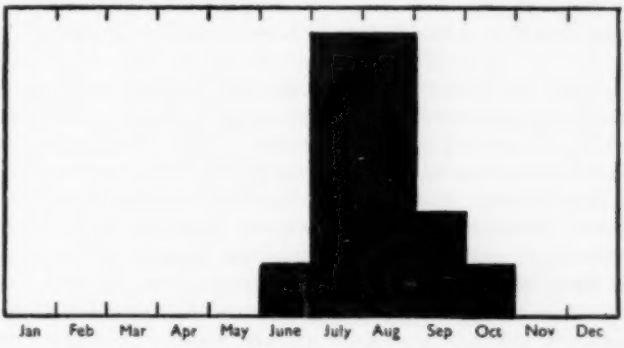

Fig. 4.—*Phacochoerus aethiopicus*. Thirty litters recorded in the Northwestern plateau areas of N. Rhodesia. Birth months calculated from observations of young under one month old.

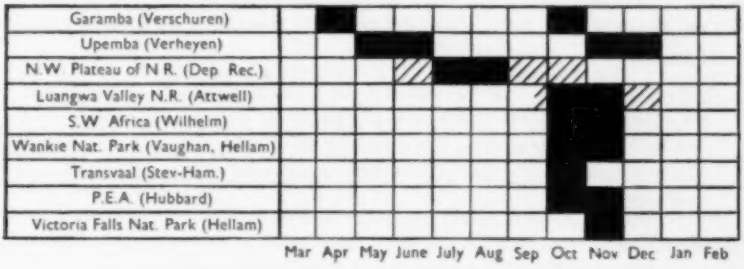
Garamba (Verschuren)
Upemba (Verheyen)
N.W. Plateau of N.R. (Dep. Rec.)
Luangwa Valley N.R. (Attwell)
S.W. Africa (Wilhelm)
Wankie Nat. Park (Vaughan, Hellam)
Transvaal (Stev-Ham.)
P.E.A. (Hubbard)
Victoria Falls Nat. Park (Hellam)
Mar Apr May June July Aug Sep Oct Nov Dec Jan Feb

Fig. 5.—*Phacochoerus aethiopicus*. Chart showing farrowing seasons in Central and Southern Africa.

saw the earliest arrivals on 25th July. In 1958, in the same area, he records that the peak of farrowing had been reached by 29th. July when " dozen of females with young " were seen ; and in the Kasempa sector of the Park on 3rd August 1959 " most sows now accompanied by young, 2–6 per litter ". In the Luangwa Valley the farrowing time is later, from late September to December, with a possible peak October–November (Attwell, *in litt.*) which agrees with areas farther south, both on the east and west of the continent (Fig. 5). In the Luangwa Valley (North) Game Reserve between mid-

November and mid-December 1959, L. D. C. Allen recorded litters estimated six to eight weeks old, which agrees with Attwell's report. Allen has drawn attention to the fact that some sows had older young than this with them, which he estimated aged about nine months, though it seems more probable that they would have been the previous season's litters, thus about a year old. I have sometimes seen sows with the previous litter as well as newly born young, though more information on the growth rate is needed before one can be absolutely sure about their ages.

There is a record from the middle Zambesi Valley, in Gwembe District, of a litter a few weeks old in November (C. W. Benson) ; of two juveniles estimated five months old in March 1959 (Hellam) ; and Uys considers November to be the peak farrowing time in this area, which thus corresponds with the Luangwa Valley.

Farther north the situation apparently changes, and it is recorded that wart hog in the Upemba area and the Garamba National Park in the Belgian Congo have two farrowing times (Verheyen, 1951 ; Verschuren, 1958). In the former locality foetuses have been found during March and April (Frechkop, 1954). In East Africa, the Cameroons, Senegal and the French Sudan the species appears to breed at any time (Roosevelt & Heller, 1922 ; Jeannin, 1936 ; Dekeyser, 1956). These places are nearer the Equator than where marked seasonal breeding has been recorded. It is possible that the occurrence of two farrowing seasons in the Belgian Congo may indicate a transition between seasonal and non-seasonal breeding. Further data is necessary to confirm or refute this.

The young are plain coloured, like the adults, and are normally born below ground in old antbear holes, which is the usual lying up place for wart hogs. According to Verheyen (1951), they remain there for about two weeks, which may be so, though very tiny juveniles are often seen out with their parents.

Mammae : no data.

Young per birth : 2–7, usually 3–4 from most N. Rhodesian data. Verheyen suggests three in younger sows and four or more with older ones. Allen (dep. rec.) has noted in the Luangwa Valley that new born litters usually number 4–7 while older ones are usually reduced to 3 or less.

Hippopotamidae

HIPPOPOTAMUS AMPHIBIUS Linn. (Hippopotamus)

Departmental records of newly born young are from April to December ; and mating or attempted mating has been seen in June, and September–October. Hubbard (1929) records a foetus estimated within two weeks of birth on the Kafue River in early August, while Stewart (dep. rec.) found one 21 inches long and 22 lb. weight near Mpika on 8th January 1959. In the Luangwa River a birth took place on land during the night of 6th–7th July 1958, and the calf was seen to enter the water with its dam at 8.30 a.m. on 7th July (W. R. Bullock, dep. rec.). Shortridge (1934) records his opinion that there is no fixed season of birth in Southwest Africa. This is also so in Garamba National Park (Verschuren, 1958), and the Cameroons (Jeannin, 1936), and

captivity records are consistent with breeding at any time. (Zuckerman, 1953 ; Asdell, 1946). This is supported by the N. Rhodesia records mentioned above, and Attwell agrees as far as the Luangwa Valley is concerned.

Mammae : 1 pair, inguinal.

Young per birth : 1 (twins may very rarely occur, though there is no confirmed instance in N. Rhodesia).

Bovidae

SYLVICAPRA GRIMMIA Linn. (Common Duiker)

Recently born young have been recorded in July, and November (dep. rec.) and foetuses in Feb. (40 mm.) ; April (" small ") ; July (full term) and September (nearly full term). From Upemba Frechkop (1954) notes foetuses in February, May, July and September ; and in Nyasaland a " large " foetus was found in December (Lawrence & Loveridge, 1953). In Livingstone Game Park Hellam (*in litt.*) states that young have been born from August to November during 1953 to 1958. The female containing the 40 mm. foetus noted above was also in lactation. Verheyen (1951) thought that in the Upemba area females may breed three times yearly. Asdell (1936) quotes Fitzsimons as stating that duiker breed all the year round in South Africa, though mainly in early spring and summer ; while Stevenson-Hamilton (1947) also thought that there is no fixed lambing time. The records given in Shortridge (1934) agree. While N. Rhodesian records might be more complete, it seems safe to say that lambing may take place at any time. The newly born lambs must be hidden for a time, though I have no definitely recorded instance of it.

Mammae - 2 pairs, inguinal.

Young per birth : 1 usually, occasionally twins (*fide* Shortridge, and Stevenson-Hamilton), though there is no recorded instance of twins in N. Rhodesia.

REDUNCA ARUNDINUM Boddaert (Reedbuck)

Information on the breeding of reedbuck in N. Rhodesia is scarce, and there are in departmental records only four instances of young below a month old reported, one estimated born in May, one in June and two in October. Other juveniles have, however, been noted from April to October ; and a foetus in October (size not recorded) and one (fully formed) in December. In the Upemba area there is a record of a foetus in January (Frechkop, 1954). Hellam's notes on Livingstone Game Park births show births from January to April. The data given by Shortridge (1934) indicate an extended lambing season. Verheyen (1951) thought that females in the Upemba area might have two young in a year. Uys has noticed that newborn young are left hidden and do not accompany the female until fairly well grown, which doubtless accounts for the few reports of young under a month old. It appears that lambing may take place throughout the year, and from Luangwa Valley observations, Attwell agrees ; while captivity records (Zuckerman, 1953) are consistent with this.

Mammae : 2 pairs, inguinal.

Young per birth : 1. Occasionally twins (Verheyen, 1951).

KOBUS ELLIPSIPRYMNUS Ogilby (Common Waterbuck)

Observations of young estimated below a month old are few, only four, with one other of a calf estimated 1½ to 2 months. These, from the Luangwa Valley, indicate births from May to about August. Matings have been seen in June and August, which, if the gestation period of 240 days given by Kenneth & Ritchie (1953) is correct, would result in births in February and April. In the Transvaal calving is recorded as usually taking place in February, but with irregularity and extending also from August to January (Stevenson-Hamilton, 1947).

While further information is needed, it is probable that there is no fixed calving season. Attwell (*in litt.*) agrees.

Roosevelt & Heller (1922) record that the female stays alone with her calf for a few days after the birth.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

KOBUS DEFASSA Rueppell (Defassa Waterbuck)

Two single foetuses have been recorded by me in the Northwestern Province, one " small " in August, and one 200 mm. in October. As with *K. ellipsiprymnus* the young are hidden for a time after birth (Uys), and this would account for the shortage of " under one month " observations. Most of the departmental records are of animals estimated at two to three months old, and these indicate a prolonged calving season from February to November, and the absence of records for January and February must be due only to the general lack of reports in those months. It seems clear then that calving may take place at any time. Roosevelt & Heller (1922) and Jeannin (1936) agree that this is so in East Africa and the Cameroons respectively, though Jeannin thought there might be a peak in the middle of the dry period. From observations in the southern part of the Kafue National Park B. L. Mitchell (*in litt.*) considers it likely that there is a peak in February and March in that area.

Mammae : 2 pairs, inguinal.

Young per birth : 1 usually, but twins seem fairly frequent, and in the Upemba Frechkop (1954) records an instance of triplets.

KOBUS VARDONI Livingstone (Puku)

In Kabompo District I have found a foetus in November which would have been born within a day or two at most. Pitman (1934) thought lambing was from May to July, and records a number of young under a month old between May and September. P. H. Morris (dep. rec.) found a new-born lamb, not yet on its feet in Kasempa District on 7th September. Uys thinks young may be born at any time of year, but adds that further observation would be needed to confirm this. There is the usual lack of reports from December to April ; but in the Luangwa Valley from 11th to 16th November 1957 Major Grimwood (dep. rec.) did not see any really young ones. Some young of unstated age have been reported in Serenje District in February, none, however,

under a month old. Mating has been seen to take place in July, August and October (dep. rec.).

Selous (quoted by Shortridge, 1934) noted November and December as the birth time, presumably in northern Bechuanaland. Verheyen (1951) thought there were two lambing seasons, June–July and January–February.

Data is therefore inconclusive, but the main lambing time appears to be May to September, with a possible peak from June to August.

The newly born young are hidden for a time, and even after starting to run with the herd they will, on being disturbed, conceal themselves in long grass while the adults make off.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

KOBUS LECHE Gray (Lechwe)

Extensive observations on the Kafue Flats have shown that while most young lechwe are born from mid-July to mid-August, the lambing season is nevertheless prolonged. The earliest recorded births were three in April, noted as "very early", and at the other extreme a decreasing number are born from September through to December. Rutting is mainly from late October to December, which would seem to indicate a gestation period of nearer eight months than seven months as given by Asdell (1946). (B. L. Mitchell and J. C. Uys, unpublished data). Shortridge (1934) records lambing in the Caprivi from July to November, which agrees approximately with the Kafue Flats. In London Zoological Gardens lechwe have bred in most months (Zuckerman, 1953). In fact February is the only month in which no birth has been recorded either in the wild or in captivity.

For the Bangweulu area (*L. leche smithemani* Lydekker) data are less complete, but there too a prolonged lambing season is recorded. W. E. Poles has seen some small juveniles in April and May, rutting in January, and recently formed foetuses in March in this area.

The newly born young are hidden for a time.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

AEPYCEROS MELAMPUS Lichtenstein (Impala)

From many records it is clear that in the northwestern plateau impala have a sharply defined lambing season, most young being born in late September and October. In the Luangwa Valley, though some may be born in October, the peak period is in November, according to Attwell (*in litt.*), and apparently from other dep. rec. may extend into December. There is one Luangwa Valley record of a lamb in April (Schultz, dep. rec.) which is well out of the usual season. In the middle Zambesi Valley, Gwembe District, B. L. Mitchell recorded thirteen young impala estimated about three to four months of age on 26th February. If this estimate is correct the season of birth there must agree with that in the Luangwa Valley, as does that of the wart hog (see above), the only other markedly seasonal breeder common to both areas.

From Fig. 6 it seems that the season in Southwest Africa is the same as in the northwestern plateau of N. Rhodesia, while in Wankie National Park and the Transvaal it is later. The Luangwa and middle Zambesi Valleys are intermediate in this.

Roosevelt & Heller (1922) believed that the doe kept to herself with her young for a short time after giving birth, while Shenton (1954) records some small lambs left on their own in the Luangwa Valley. I have put up a newly born impala from an anthill, where it was lying quite alone. Nevertheless I do not think the time from birth until joining the herd can be very long, as all the season's crop of young can be seen together with the herd when still very tiny. When such a herd is disturbed the young ones often lead the flight, then appearing like a female herd in miniature, as they are remarkably like the adults in everything except size, and in the males lacking horns. While the adults are feeding, the small ones may be left a short distance away resting together in the shade, usually with one or two adult females watching over them.

Mammae : 2 pairs inguinal.

Young per birth : 1, or sometimes twins. (Asdell 1946, and dep. rec.) There is no data on the frequency of twin births, however.

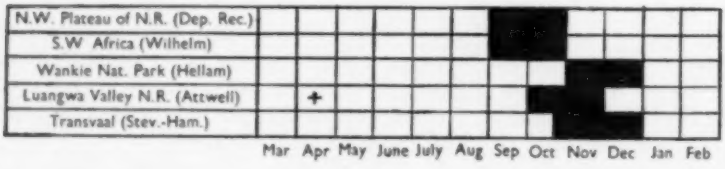
N.W. Plateau of N.R. (Dep. Rec.)
S.W Africa (Wilhelm)
Wankie Nat. Park (Hellam)
Luangwa Valley N.R. (Attwell)
Transvaal (Stev.-Ham.)
Mar Apr May June July Aug Sep Oct Nov Dec Jan Feb

Fig. 6.—*Aepyceros melampus*. Chart showing birth seasons in Central and Southern Africa.

HIPPOTRAGUS EQUINUS Desmarest (Roan Antelope)

Pitman (1934) was uncertain as to the exact calving season, but recorded some calves born in April and May. Uys has noted May as a time when a number of roan are born. Departmental records of young under a month old in the northwestern plateau up to and including 1959, are mostly from April to August, with one in October and one in November. From December to April the lack of data may be due only to the lack of reports for the period, though there are several reports of herds in September and October of which only one includes a small calf. Attwell has noted newly born young in the Luangwa Valley in September, and on the Nyika plateau in November. (Attwell *in litt.*).

Verheyen (1951) thought the species bred all the year round in the Upemba area, but with a peak period of birth from February to May. Jeannin (1936) states that mating takes place in the dry cold season in the Cameroons. Asdell (1946), perhaps combining Shortridge's records and others from farther south-east, stated there was apparently no fixed breeding season.

Data for N. Rhodesia are inconclusive, and more are needed, especially during the rains.

Newly born calves are hidden for a time after birth (Uys, Savory).

Mammae : 2 pairs, inguinal.

Young per birth : 1.

HIPPOTRAGUS NIGER Harris (Sable Antelope)

Uys considers that young sable are born in the Kafue National Park mostly from July to September. Many births calculated from " under one month old " records fall between June and September, but Shenton records calves in the Kafue National Park believed born in January, and there is also a record of a birth in March (locality not recorded) and one in Kalomo District in October. In Livingstone Game Park calving has been from January to March in the years 1953 to 1957, six to eight births taking place annually (Hellam, *in litt.*). In the Caprivi Wilhelm's records (quoted by Shortridge) indicate calving from December to January. As with the roan antelope N. Rhodesian data at present are inconclusive, and not much in accord with records from adjacent territories (Fig. 7). For example Verheyen (1951) gives the rains as the calving time, while, apart from those of the semi-captive animals in the Livingstone Park, N. Rhodesian records are mainly in the dry season, in fact between the peaks in April–May and October–November given by Verheyen.

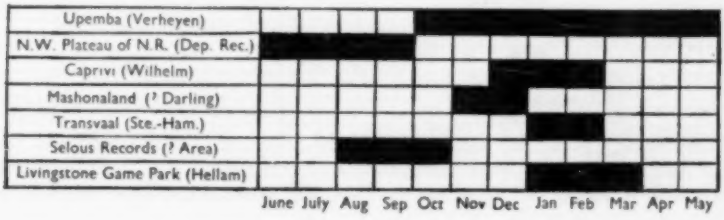
Upemba (Verheyen)
N.W. Plateau of N.R. (Dep. Rec.)
Caprivi (Wilhelm)
Mashonaland (? Darling)
Transvaal (Ste.-Ham.)
Selous Records (? Area)
Livingstone Game Park (Hellam)
June July Aug Sep Oct Nov Dec Jan Feb Mar Apr May

Fig. 7.—*Hippotragus niger*. Chart of calving seasons in Central and Southern Africa.

Uys has observed that the calves run with the herd more or less from birth. Newly born young are very light in colour.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

ALCELAPHUS LICHTENSTEINI Peters (Lichtenstein's Hartebeest)

Fig. 8 shows ninety-one births in the northwestern plateau calculated from " under one month " records, up to and including 1958. All other observations confirm that July is undoubtedly the peak calving time and that the young are generally born within a short period, though early calves may make their appearance in June, and late ones in September (possibly even October, though this would be unusual). Uys noted a pair mating in Kasempa District in November, and suggests a gestation period of ± 237 days, which agrees closely with Stevenson-Hamilton's estimate (Kenneth & Ritchie, 1953).

From the Luangwa Valley the only two records of young under a month old are in October and November, but Attwell (*in litt.*) confirms that these months are in fact the main calving time there. From Fig. 9 it can be seen that the Upemba area corresponds with the northwestern plateau of N. Rhodesia while the Luangwa Valley agrees with records from farther south.

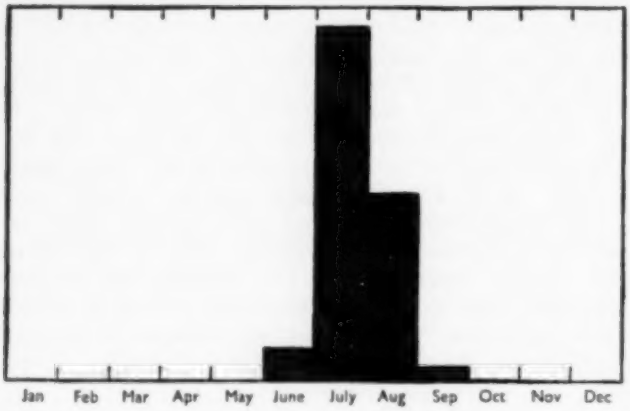

Fig. 8.—*Alcelaphus lichtensteini.* Ninety-one births in the Northwestern plateau areas of N. Rhodesia calculated from observations of young under one month old.

Infant hartebeests are concealed after birth for a short time, the cows often remaining on guard near by. Two or more may be thus hidden, and I believe they may be left on their own at times even after starting to run with the herd, for I have seen quite strong calves together in a little group, as well as herds without calves at times when the cows must have already given

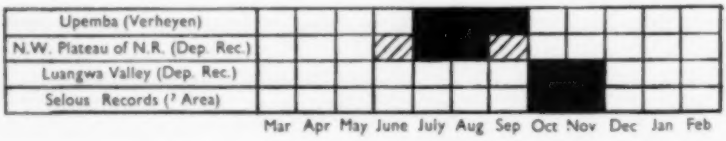

Fig. 9.—*Alcelaphus lichtensteini.* Chart of calving seasons in Central Africa.

birth. By the time they are two to three months of age hartebeest have spike-like horns, without curves, about 4 inches long. I noticed a calf of this age showing the dark smudge behind the shoulder, which is characteristic of the adults, and is believed due to the rubbing of the face gland on the body at this point, leaving a dark sticky deposit. It seems, then, that this gland is functional at an early age. Young hartebeest are much lighter coloured than the adults.

Mammae : 1 pair, inguinal.

Young per birth : 1 usually. There is some evidence that twins may be born occasionally.

CONNOCHAETES TAURINUS Burchell (Blue Wildebeest)

The nominate race inhabits the western parts of the northwestern plateau, and many records indicate calving mainly in September and October, with early births in August and late ones in November. However, B. L. Mitchell believes that in the Southern Province the calving is late August to September in the Isoberlinia and Mopane areas of Kalomo and western Namwala Districts, and October to November on the open flood plains of the Kafue Flats (B. L. Mitchell, *in litt.*). This is interesting because Selous found that in 1879 calving was in September in the Chobe area, but not until November in the Mababe Flats, not far distant (quoted by Shortridge, 1934). In the Transvaal Stevenson-Hamilton has noted that in the Kruger Park young are born from early December to mid-January, but in November 30 miles west of the present boundary, which is presumably because the new grass appears there rather earlier. Eloff (1959) notes irregularity in calving in the Kalahari Gemsbok National Park in 1957, and discusses the question in relation to observations on variation in birth times made by M. H. Cowie in Kenya. It seems then that in many, if not all, parts of its range the species, while strongly seasonal in calving, may show variations due to quite local conditions (Fig. 10). Further investigation of this is desirable.

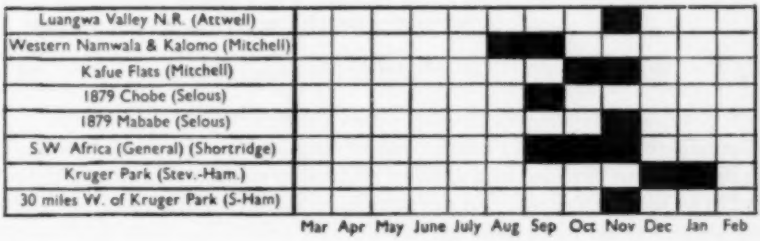
Luangwa Valley N.R. (Attwell)
Western Namwala & Kalomo (Mitchell)
Kafue Flats (Mitchell)
1879 Chobe (Selous)
1879 Mababe (Selous)
S.W. Africa (General) (Shortridge)
Kruger Park (Stev.-Ham.)
30 miles W. of Kruger Park (S-Ham)
Mar Apr May June July Aug Sep Oct Nov Dec Jan Feb

Fig. 10.—*Connochaetes taurinus*. Chart of calving seasons in Central and Southern Africa.

It is difficult to account for Pitman's belief that the young are dropped "mainly in June and July" (Pitman 1934). All other evidence is against this, and it is easier to note the appearance of the first young in this species than almost any other. There are in fact several notes in the departmental records of new born calves not yet on their feet, as well as numerous herds without small calves in June and July.

Records of births among *C. t. cooksoni* Blaine, which occurs in the Luangwa Valley, are fewer, but such as they are indicate a later season than on the plateau. Attwell (*in litt.*) gives November as the main calving month, and Shenton records "possibly as late as December". Allen (dep. rec.) has reported numerous recently born calves in the Luangwa Valley (North) Game Reserve in November–December 1959.

Wildebeest calves are much lighter coloured than the adults, and they run with the herd from birth. They are very swift even when a few hours old,

and show remarkable endurance. Sherfield (dep. rec.) has noted that with one new born calf the time from its first attempt to stand until it *ran off with the herd* was less than five minutes.

Mammae : 1 pair, inguinal.

Young per birth : 1.

DAMALISCUS LUNATUS Burchell (Tssessebe)

Records for N. Rhodesia are few, but indicate a season of birth just as for the hartebeest, i.e. mostly July, with early calves born a little earlier, and late ones in August or September. Farther southeast and southwest calving is later (Fig. 11).

Mammae : No data, but presumably would be 1 pair, inguinal, as in *Alcelaphus lichtensteini* and *Connochaetes taurinus*.

Young per birth : 1.

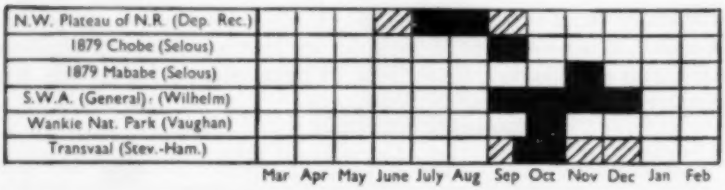
N.W. Plateau of N.R. (Dep. Rec.)
1879 Chobe (Selous)
1879 Mababe (Selous)
S.W.A. (General). (Wilhelm)
Wankie Nat. Park (Vaughan)
Transvaal (Stev.-Ham.)
Mar Apr May June July Aug Sep Oct Nov Dec Jan Feb

Fig. 11.—*Damaliscus lunatus*. Chart of calving seasons in Central and Southern Africa.

TRAGELAPHUS SCRIPTUS Pallas (Bushbuck)

Records of foetuses and newly born young are few, but indicate lambing from February to October, and absence of data for the other months is probably only due to lack of reports. In the Garamba National Park Verschuren (1958) found there was no fixed lambing season, and Sclater (quoted by Shortridge, 1934) stated that the species bred all the year round in the Port Elizabeth, but farther inland the breeding season was mainly in October–February. It is not clear in which sense Sclater was using the term " breeding season ". Stevenson-Hamilton (1947) gave September to March as the lambing season in the Transvaal, while Jeannin (1936) considers it to be the dry season in the Cameroons.

While, from published records, there is the probability of a peak lambing period, it seems that the species may lamb in any month. Attwell agrees from Luangwa Valley observations.

I have no definite information on the point, but the lambs are doubtless hidden for a time after birth.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

TRAGELAPHUS SPEKEI Sclater (Sitatunga)

I have found nearly full term foetuses in August, October (two instances), and November ; and less developed foetuses in October and November. Davi-

son (1950) records that young are born in the Chobe area in June and July. Mr T. R. Evans, of the Veterinary department, has recorded a young one believed under one month old in Serenje District in March, and also reports that local native information is that young are born at the beginning and end of the rains. Pitman's record of newly born lambs on Nkose Island, Uganda (Pitman, 1928), appears an isolated observation, not necessarily indicating a definite season of birth.

On the whole it seems probable that young may be born at any time of year, but more data are needed to be certain.

The lambs are concealed among reeds for a time after birth (Davison, 1950).

Mammae : 2 pairs inguinal.

Young per birth : 1.

TRAGELAPHUS STREPSICEROS Pallas (Kudu)

Definite dates on which births have been recorded are 26th January in Lusaka District (G. E. Taylor), a calf still wet from birth rescued alive from a honey badger (*Mellivora capensis* Schreber) ; and 21st February, in Lundazi District (O. Charlton), a calf either just born or just about to be, killed together with its parent by a hyaena (*Crocuta crocuta* Erxleben). A foetus collected in Mazabuka District in November (C. W. Benson) would probably have been born in late December or early January. Records of young under one month old include February, March, April, May, June, July, September, October and November, so it is clear that calving may take place at any time. Wilhelm (quoted by Shortridge, 1934), and Stevenson-Hamilton (1947) seem to imply that there may be a definite season for calving, but in the light of the foregoing data this seems doubtful. From Luangwa Valley observations Attwell agrees that young may be born at any time of year.

A newly born calf was seen hidden under a bush (dep. rec.) and I have twice seen a female alone with her recently born young.

Mammae : 2 pairs, inguinal.

Young per birth : 1.

TAUROTRAGUS ORYX Pallas (Eland)

Pitman (1934) was uncertain when elands calved in N. Rhodesia, but noted many small calves in July and August. Uys is inclined to think February to July is the main birth time, while Carr (dep. rec.) has noted " April onward " in the Luangwa Valley. Available information indicates a peak period from June to August, though there are other records in April, September and November, and one in Livingstone Game Park in March. In 1959 in a herd of about eighty animals on Lochinvar Ranch, Mazabuka District, the ranch manager, Mr Van Zyl, reported calves born as follows : nine in January or February, six in March and eleven in April. A single calf under one month old was seen there with a cow during November 1959 (W. P. Crowcroft) but whether from this same herd or not is not known.

Selous' observation (quoted by Shortridge, 1934) that elands calve in S. Rhodesia from June to August agrees, as far as it goes with the N. Rhodesia

time. Stevenson-Hamilton (1947) states that in southeastern Africa elands calve from March to May (mainly in April), and again early August to the beginning of November. In the southern part of its range he believes it unlikely that many calves are born in the cold months of June and July.

In N. Rhodesia it seems likely that calves may be born at any time. Captivity records (Zuckerman, 1953) show that elands can calve at any time of the year.

N. Rhodesian records seem to indicate that, irrespective of the actual month, several cows in a herd may calve about the same time. There are many instances of several young of uniform age seen together. Morris (dep. rec.) reported in the Kasempa sector of the Kafue National Park that one herd in August included ten calves, all estimated about two months old ; while just on a month later he saw a herd of forty-seven animals without a single young calf. Further information on this is needed.

In view of the wandering habits of eland it seems probable that the calves accompany the herd almost from birth, though Crowcroft's observation of a very small calf on Lochinvar Ranch with its parent may indicate that at least for a short time the cow remains apart from the herd after giving birth.

Mammae : 2 pairs, inguinal.

Young per birth : usually 1, but in the London Zoological Gardens twins have been born in about 2 per cent of the total births. (Zuckerman, 1953).

SYNCERUS CAFFER Sparrman (African Buffalo)

Records appear to indicate calving throughout the year, which accords with data from the Garamba National Park and Upemba (Verheyen, 1951 ; Verschuren, 1958), and the Cameroons (Jeannin, 1936). Information from other areas implying a limited season of birth (e.g. Shortridge, 1934) may therefore be incomplete, though there is probably a peak period of calving. In the Luangwa Valley there may be a peak in June and July (W. E. Poles, dep. rec.) ; while Verheyen (1951) gives April to June for the Upemba ; and Jeannin (1936) considers the end of the dry season the peak period in the Cameroons.

In London African buffalo have calved in all months (Zuckerman, 1953).

The young are believed to accompany the herd more or less from birth (Verschuren, 1958).

Mammae : 2 pairs, inguinal.

Young per birth : 1.

Giraffidae

GIRAFFA CAMELOPARDALIS Linn. (Giraffe)

Giraffe are in N. Rhodesia limited to Barotseland between the Zambesi and Mashi Rivers, and the Luangwa Valley, and data on breeding are few. Attwell and Morris from Luangwa Valley observations believe that calves are born at the beginning of the rains, i.e. about October–November. In the Livingstone Game Park captive animals, believed originally from Barotseland,

have calved in February, July and September; while those at present in the Park were seen to mate in "almost every month" during 1958 (Hellam *in litt.*). Wilhelm, presumably for the Caprivi, thought March onwards was the calving time, July and September being the mating season (quoted by Shortridge, 1934). The gestation period is fourteen to fifteen months (Kenneth & Ritchie, 1953), so Wilhelm's impressions may be incorrect in one respect of the other. Stevenson-Hamilton (1947) states that giraffe are born in the Transvaal from about October onwards for about two or three months. Neumann (quoted by Shortridge, 1934) thought there was no definite calving season, which in view of Hellam's note that mating has been seen almost throughout the year, and the apparent discrepancy in Wilhelm's account, may be correct. In London giraffes have calved in all months from February to October (Zuckerman, 1953).*

Mammae : 1 pair, inguinal (not 2 pairs) (Shortridge, 1934).

Young per birth : 1 usually. Rarely twins according to Vaughan-Kirby (quoted by Shortridge, 1934).

CARNIVORA

Canidae

LYCAON PICTUS Temminck (Wild Dog)

There are several records of new born cubs in Northern Rhodesia. In Mporokoso District Stokes (dep. rec.) had two litters brought to him in May, estimated two weeks old. I have seen cubs at Mazabuka believed born in the last week of May, 1952, and the next year obtained others there about the same time. In 1959 eight were brought to me at Kabompo which had been born about the third week of June. These were undoubtedly all of one litter. C. W. Benson has seen cubs at Kasama in early July which were under one month old, and in the Mumbwa District he got information of three litters (total 15 cubs), which were in August estimated at two to three weeks of age. In the Southern Province B. L. Mitchell has recorded cubs about four to six weeks old on 23rd June. Three cubs collected by W. E. Poles in the Luangwa Valley on 21st September, and now in the National Museum, Bulawayo, were "certainly not less than two months old" (M. Paterson, *in litt.*). From Mwinilunga District I have seen a cub only two or three days old, which was killed on or about 6th July.

As there are no records at all in any other period of the year, it is apparent that May to July is the usual whelping time for wild dogs in N. Rhodesia.

Stevenson-Hamilton (1947) has remarked on the practice of two or more bitches littering in the same hole. The cubs from Zimba and one group from Mazabuka were in each case believed to comprise two litters. This often makes it difficult to tell the individual litter sizes.

The cubs are born blind; usually, though not always, below ground in old antbear holes. At birth they are black and white, lacking yellow pigment,

* Innis (*Proc. zool. Soc. Lond.* Vol. 131, (1958), 245-278) states that in the Transvaal, giraffe have no fixed season of birth; and she confirms that twin births sometimes occur.

time. Stevenson-Hamilton (1947) states that in southeastern Africa elands calve from March to May (mainly in April), and again early August to the beginning of November. In the southern part of its range he believes it unlikely that many calves are born in the cold months of June and July.

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N. Rhodesian records seem to indicate that, irrespective of the actual month, several cows in a herd may calve about the same time. There are many instances of several young of uniform age seen together. Morris (dep. rec.) reported in the Kasempa sector of the Kafue National Park that one herd in August included ten calves, all estimated about two months old ; while just on a month later he saw a herd of forty-seven animals without a single young calf. Further information on this is needed.

In view of the wandering habits of eland it seems probable that the calves accompany the herd almost from birth, though Crowcroft's observation of a very small calf on Lochinvar Ranch with its parent may indicate that at least for a short time the cow remains apart from the herd after giving birth.

Mammae : 2 pairs, inguinal.

Young per birth : usually 1, but in the London Zoological Gardens twins have been born in about 2 per cent of the total births. (Zuckerman, 1953).

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Records appear to indicate calving throughout the year, which accords with data from the Garamba National Park and Upemba (Verheyen, 1951 ; Verschuren, 1958), and the Cameroons (Jeannin, 1936). Information from other areas implying a limited season of birth (e.g. Shortridge, 1934) may therefore be incomplete, though there is probably a peak period of calving. In the Luangwa Valley there may be a peak in June and July (W. E. Poles, dep. rec.) ; while Verheyen (1951) gives April to June for the Upemba ; and Jeannin (1936) considers the end of the dry season the peak period in the Cameroons.

In London African buffalo have calved in all months (Zuckerman, 1953).

The young are believed to accompany the herd more or less from birth (Verschuren, 1958).

Mammae : 2 pairs, inguinal.

Young per birth : 1.

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Giraffe are in N. Rhodesia limited to Barotseland between the Zambesi and Mashi Rivers, and the Luangwa Valley, and data on breeding are few. Attwell and Morris from Luangwa Valley observations believe that calves are born at the beginning of the rains, i.e. about October–November. In the Livingstone Game Park captive animals, believed originally from Barotseland,

have calved in February, July and September; while those at present in the Park were seen to mate in "almost every month" during 1958 (Hellam *in litt.*). Wilhelm, presumably for the Caprivi, thought March onwards was the calving time, July and September being the mating season (quoted by Shortridge, 1934). The gestation period is fourteen to fifteen months (Kenneth & Ritchie, 1953), so Wilhelm's impressions may be incorrect in one respect of the other. Stevenson-Hamilton (1947) states that giraffe are born in the Transvaal from about October onwards for about two or three months. Neumann (quoted by Shortridge, 1934) thought there was no definite calving season, which in view of Hellam's note that mating has been seen almost throughout the year, and the apparent discrepancy in Wilhelm's account, may be correct. In London giraffes have calved in all months from February to October (Zuckerman, 1953).*

Mammae: 1 pair, inguinal (not 2 pairs) (Shortridge, 1934).

Young per birth: 1 usually. Rarely twins according to Vaughan-Kirby (quoted by Shortridge, 1934).

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As there are no records at all in any other period of the year, it is apparent that May to July is the usual whelping time for wild dogs in N. Rhodesia.

Stevenson-Hamilton (1947) has remarked on the practice of two or more bitches littering in the same hole. The cubs from Zimba and one group from Mazabuka were in each case believed to comprise two litters. This often makes it difficult to tell the individual litter sizes.

The cubs are born blind; usually, though not always, below ground in old antbear holes. At birth they are black and white, lacking yellow pigment,

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which develops later, in this respect exactly resembling tricolor foxhound puppies.

Mammae : 6 or 7 pairs, abdominal.

Young per birth : 2–8.

Felidae

PANTHERA PARDUS Linn. (Leopard)

Data on breeding in N. Rhodesia is scanty. I have seen cubs from Kasama and Choma Districts estimated born in November, and have found two small foetuses (about 25 mm. long) in a female at Mazabuka on 6th January. Uys, from observations in the Southern Province, is inclined to think there may be a more or less regular whelping season about June–July, while B. L. Mitchell (also in Southern Province) thinks July to September. However, accepting the maximum gestation period of 105 days (Kenneth & Ritchie, 1953) the Mazabuka leopardess mentioned could not have given birth later than April, and in fact would probably have done so before that time. Verheyen (1951) suggests that the female may breed twice in a year, but admits this is based only on native information. Stevenson-Hamilton (1947) considers litters are generally born in South Africa during winter and spring, but notes that no definite rule can be laid down. Jeannin (1936) considers that in the Cameroons mating may take place at any time of year. Shortridge (1934) also suggested there was no fixed season of birth.

While more data is needed the probability is that in N. Rhodesia cubs may be born at any time of the year.

Leopard cubs are born blind (Shortridge, 1934). There are several N. Rhodesian records of single quite young cubs unaccompanied by the parent (Uys).

Mammae : 2 pairs, abdominal.

Young per birth : 3–6, usually 3 (Haagner, 1920). But in N. Rhodesia may be only two, and in London Zoological Gardens only 1–3 has been recorded (Zuckerman, 1953).

PANTHERA LEO Linn. (Lion)

Data from N. Rhodesia confirms published records from elsewhere that litters may be born at any time of year (Shortridge, 1934 ; Stevenson-Hamilton, 1947 ; Asdell, 1946 ; Roosevelt & Heller, 1922 ; Jeannin, 1936 ; Zuckerman, 1953). Actual N. Rhodesia records are of litters estimated born in March, April, June, July and December, and of foetuses (1 × 3, about ½ developed) in April.

Lion cubs open their eyes on the sixth day after birth (Haagner, quoted by Shortridge, 1934).

Mammae : 2 pairs, lower abdominal.

Young per birth : 3–4 usually.

ACINONYX JUBATUS Schreber (Cheetah)

Records of breeding are few. A cub estimated not more than two weeks old from Lusaka District was seen by me in March at Chilanga. C. W. Benson

records cubs which had certainly been born in November in Fort Jameson District. A specimen from Solwezi District, now in the Bulawayo Museum, about four months old when killed, was estimated to have been born in March or April. Stevenson-Hamilton (1947) records litters in the Transvaal from August to November, and Shortridge (1934) cites a record from Wilhelm of a litter in Southwest Africa born in December or January.

Present data is insufficient to indicate whether there is a regular season of birth or not.

The cubs are born blind (Stevenson-Hamilton, 1947). The long mantle of blue-grey hair along the back of young cheetahs is well known (see especially Webb, 1948, and Holdstock, 1947) but in the very tiny cub examined at Chilanga the mane was absent (Ansell, 1957).

Mammae : No data.

Young per birth : 2–4 usually (Stevenson-Hamilton, 1934).

DISCUSSION

Much more data is needed on all aspects of the breeding of the species dealt with, but certain provisional conclusions may be reached.

Ungulates.

While the ungulates vary from permanently polyoestrus, breeding at any time of year, to those in which the season of birth is very sharply limited to a definite period, the latter is not usual, only the two species of pigs and four antelopes falling into this category.

The markedly seasonal breeders among the Bovidae are all gregarious, and three of them are closely related, belonging to the same subfamily, where subfamily is used as a taxonomic category, or the same tribe according to Simpson's classification (Simpson, 1945). These are *Alcelaphus lichtensteini*, *Connochaetes taurinus*, and *Damaliscus lunatus*. The other seasonal breeder is *Aepyceros melampus*.

Though the two suids, *Potamochoerus porcus* and *Phacochoerus aethiopicus* are in Northern Rhodesia markedly seasonal in their farrowing, the latter species gives birth farther north at any time, and in parts at least of the Belgian Congo may have two farrowing seasons, which may be a transitional stage.

The very largest land mammals, *Loxodonta africana*, *Diceros bicornis*, and *Hippopotamus amphibius* give birth at any time of the year.

Among the Bovidae the solitary or semi-gregarious antelopes *Sylvicapra grimmia*, *Redunca arundinum*, *Tragelaphus scriptus*, *T. spekei* and *T. strepsiceros* are believed to have their young at any time, and so also do the gregarious waterbucks, *Kobus ellipsiprymnus* and *K. defassa*, and the highly gregarious buffalo, *Syncerus caffer*.

Though the zebra, *Equus burchelli*, may foal in any month it has such a definite peak time (Fig. 1) as to be practically seasonal, though to be accurate it might be better to regard the species as intermediate between the more markedly seasonal and the random breeders.

It seems probable that something similar may apply to those species of antelope on which present information is indefinite, *Kobus leche*, *K. vardoni*,

Hippotragus niger, *H. equinus* and *Taurotragus oryx*. While these possibly calve in any month there may nevertheless be such a marked peak period as to constitute virtually a season.

The phenomenon of several cows of a herd apparently calving about the same time, irrespective of the actual month, appears very definite in the eland, *T. oryx*, and is worth further investigation.

In the wildebeest, *Connochaetes taurinus*, calving, though strictly seasonal, may vary with purely local conditions, and this has been noted in several parts of the species range (Fig. 10).

Variation of the birth months in different parts of the continent among the strictly seasonal breeders seems up to now to have been given insufficient attention. It is however clearly indicated by the data noted above. In general the farther south the later the birth season (in countries south of the Equator). This is brought out in Figs. 3, 5, 6, 9 and 10, and further in the following extract of a letter from Mr L. E. Vaughan who states : " I also notice breeding to be later in the year here (Wankie National Park, Southern Rhodesia) by about two months than at Namwala, curious because it cannot be above 250 miles as the crow flies. For instance wart hogs do not have their young till early October, while up there they litter in mid-August. Also hartebeest there calve in July, and the corresponding tssessebe here not till October ".

Regarding seasonal breeding the low-lying Luangwa and middle Zambesi Valleys correspond better with more southern areas than with the north-western plateau. It is not known with which the Eastern Province plateau corresponds, but it may be with the northwestern plateau. It must, however, be stated that these points concern only some of the seasonal breeders, for only the wart hog, *P. aethiopicus* is common to all these localities, as is shown in the following table.

Distribution of strictly seasonal breeders.

Species	N.W. plateau.	E.P. plateau.	Luangwa Valley	Mid-Zambesi Valley.
Phacochoerus aethiopicus	Present	Present	Present	Present
Aepyceros melampus	Present	Virtually absent	Present	Present
Alcelaphus lichtensteini	Present	Present	Present (few)	Absent in valley floor
Connochaetes taurinus	Present	Virtually absent (rare stragglers only)	Present	Absent
Damaliscus lunatus	Present	Absent	Absent	Absent

Present knowledge is insufficient to assess possible correlation of climatic and other factors with birth times in the seasonal breeding species. Even less is known of possible fluctuations in intensity of breeding in the non-seasonal.

As far as is known, the young of all solitary and semi-gregarious bovids are hidden for some time after birth, and so are the young of some gregarious

species. Among the strictly seasonal breeders the hartebeest (*A. lichtensteini*) hide the calves at birth, while the impala (*A. melampus*) may do so. The wildebeest (*C. taurinus*) calves on the other hand run with the herd from birth. It is not known whether or not the young tsessebe (*D. lunatus*) are concealed at birth.

Carnivora

Lycaon pictus, the only canine considered, is seasonal in whelping in N. Rhodesia, and doubtless, as with the others of its family, is monoestrus. Among the larger felids *Panthera leo* and probably *P. pardus* may have their young at any time of year, but data on *Acinonyx jubatus* is insufficient to form any conclusion.

General

It is unfortunate that past observations on the breeding of the larger African mammals have not been more extensive, and that detailed information should be limited to so few areas. It will never be possible to remedy this completely as future studies must necessarily be confined to the relatively small areas where game is still plentiful. Where such investigations can be carried out they must inevitably be largely limited to field observations. It is out of the question to examine large numbers of pregnant females as can be done in breeding studies of plentiful and easily procurable small mammals. It is, however, suggested that more records of young under one month old, as noted in the N. Rhodesia game reports would materially add to existing knowledge ; and this should where possible be supplemented by records of foetal material. The following N. Rhodesian Bovidae have been omitted from detailed consideration above due to lack of data. *Cephalophus sylvicultor* Afzelius, *C. monticolus* Thunberg, *Raphicerus campestris* Thunberg, *R. sharpei* Thomas, *Ourebia ourebi* Zimmermann and *Oreotragus oreotragus* Zimmermann. All these are solitary or semi-gregarious, and therefore probably have no fixed season of birth.

REFERENCES

Anon (1956). Annual Report, Game Section, Dept. of Lands, Mines and Surveys, S.R. Govt.

Ansell, W. F. H. (1957). Northern Rhodesia's protected animals. *Afr. Wild Life* **11** : 19.

Asdell, S. A. (1946). *Patterns of mammalian reproduction*. Ithaca : Comstock.

Davison, E. (1950). The home of the sitatunga—a maze of reeds. *Afr. Wild Life* **4**, No. 1 : 57.

Dekeyser, P. L. (1956). *Les mammifères de l'Afrique Noire Française*. Ed. 2. Dakar : I.F.A.N.

Eloff, F. C. (1959). Observations on the migrations and habits of the antelopes of the Kalahari Gemsbok National Park, Part I. *Koedoe* No. 2 : 1–29.

Frechkop, S. (1954). *Explor. Parc Nat. l'Upemba* Fasc. 14, Mammiferes. Inst. des Parcs Nationaux du Congo Belge, Brussels.

Haagner, A. (1920). *South African mammals*. London : Witherby.

Holdstock, M. (1947). Cheetah cubs are fun. *Afr. Wild Life* **11** : 335.

Hubbard, W. D. (1929). Further notes on the mammals of Northern Rhodesia and Portuguese East Africa. *J. Mammal.* **10** : 294.

Jeannin, A. (1936). *Les mammifères sauvages du Cameroun*. Paris : Lechevalier.

Kenneth, J. H. & Ritchie, G. R. (1953). *Gestation periods*, Ed. 3. Edinburgh : Commonwealth Bureau of Animal Breeding and Genetics.

Lawrence, B. & Loveridge, A. (1953). Mammals from Nyasaland and Tete. *Bull. Mus. comp. Zool. Harv.* **110** : 1–80.

Perry, J. S. (1952). The growth and reproduction of elephants in Uganda. *Uganda J.* **16** : No. 1.

PITMAN, C. R. S. (1928). Note on Nkosi Island and its sitatunga. *Proc. zool. Soc. Lond.* **1928** : 655.

PITMAN, C. R. S. (1934). *Report on a faunal survey of N. Rhodesia.* Livingstone : Govt. Printer.

POPPLETON, F. (1957). An elephant birth. *Afr. Wild Life* **11** : 106.

ROOSEVELT, T. & HELLER, E. (1922). *Life histories of African game animals.* London : John Murray.

SHENTON, J. B. (1954). Oddities from the Luangwa Valley, N. Rhodesia. *Afr. Wild Life* **8** : 201.

SHORTRIDGE, G. C. S. (1934). *The mammals of Southwest Africa.* London : Heinemann.

SIMPSON, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* **85** : 1–350.

STEVENSON-HAMILTON, W. (1947). *Wild life in South Africa.* London : Cassel.

VERHEYEN, R. (1951). *Contribution a l'étude éthologique des mammifères du Parc National de l'Upemba.* Brussels : Inst. des Parcs Nationaux du Congo Belge.

VERSCHUREN, J. (1958). *Ecologie et Biologie des grands mammifères du Parc National de Garamba.* Brussels : Inst. des Paris Nationaux du Congo Belge.

WEBB, C. S. (1948). Colour changes in animals. *Zoo Life* **3**, No. 1, Spring 1948 (p. 8).

ZUCKERMAN, S. (1953). The breeding seasons of mammals in captivity. *Proc. zool. Soc. Lond.* **122** : 828.

APPENDIX

Form of Game Report as used for recording of data on the larger mammals by Game Officers in Northern Rhodesia.

GAME REPORT

No. .....

Species..... Date and time seen.....

Exact locality (give altitude also where of interest).....

.....

Composition of herd :

Males..... Females..... Undetermined Sex..... Juveniles..... Total.....

Number of juveniles definitely under one month old.....

In case of elephant, number of tuskless Males.....Females.....Juveniles.....

Indications of mating .....

Nature of country in which seen.....

.....

Type of vegetation on which browsing or grazing.....

.....

Other species associated with herd.....

Notes on recognition of individuals (relate to previous report), condition, or other points of interest

.....

.....

.....

.....

Date..... Signature..... Designation.....

SOME INTERESTING PATHOLOGICAL CASES IN AMPHIBIANS

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[Accepted 10th November 1959]

(With 43 figures in the text)

Published literature on amphibian pathology is extremely sparse and our knowledge of the amphibian reaction to the factors commonly causing disease in these animals is as yet very incomplete. Apart from accidents, not included in this survey, the main causes of morbidity in amphibians are parasites, tumours, inflammatory conditions and fungal infestation.

Presented here are twenty-three case histories of amphibians either freshly caught and found to be diseased or falling ill while being kept in captivity.

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INTRODUCTION

The morbid anatomy and the histology of disease in the Amphibia can unfortunately not be studied as systematically as that of man or the higher vertebrates. For example, a research worker intending to investigate the pulmonary carcinoma of frogs might only have an opportunity to examine, in his lifetime, two or three cases, and though the rarity of this condition makes it so much more interesting, no general conclusions can be drawn until a large number of cases have been described.

Other diseases occur in the Amphibia, many of which are not as rare as renal or pulmonary carcinoma, but investigation in this field is made more difficult by one major factor: the behaviour of the animals themselves. Amphibians are naturally retiring creatures. They are mostly nocturnal and, being highly adapted to their natural environment, few display the signs of health and disease best in captivity. When they become ill they retire immediately to any available inaccessible place, frequently to die there unnoticed. Species imported from the tropics have necessarily to be kept in suitably heated cages in order that they may survive, and in consequence, unless the death of the specimen is quickly discovered, rapid post mortem changes make it useless for any further investigation owing to the quick rate of decomposition. As a result, the causes of a valuable specimen's refusal to feed, or the cause of its death, remain too often unknown. With our

present lack of knowledge of amphibian diseases, treating a sick animal becomes an unpredictable experiment.

How little is known of the biology and pathology of amphibians is reflected by the fact that, although Salientia and urodeles are kept in large numbers by both laboratories and amateurs all over the world, veterinary textbooks make only passing reference to them, while the few works devoted to herpetology, only briefly comment on " diseases ". Even if amphibians do not lend themselves easily to experimental and systematic treatment of their pathology, it should be possible for those laboratories keeping them in large numbers to collect relevant data by isolating diseased animals and transferring them post mortem to the refrigerator for further study. The material presented here may demonstrate the rewarding, interesting and often surprising results which may be obtained by this practice. It is based on Amphibia kept in a laboratory devoted mainly to Pregnancy Tests by the Hogben method. Apart from a large colony of *Xenopus laevis* D., other amphibians, both Salientia and Caudata were kept for longer or shorter periods. Occasionally a request printed in the *Journal of Herpetology* has produced a specimen which succumbed in the collection of a reader even though every care had been given to it.

If the small number of twenty-three cases presented here can be taken as providing a fair average sample of amphibian health and disease, it would seem that these animals are, on the whole, hardy creatures, not subject to many natural diseases. They may be handicapped by developmental errors or by injuries sustained in fights or accidents, but the number of ordinary transitory diseases affecting them seems to be very small. The fact that they spend their life either in or very near the water, in an environment which is also that of many of their parasites, exposes them to hazards from the moment they hatch. Sometimes symbiosis exists between host and parasite ; in other instances the host exhibits a strong defensive reaction, but often the parasitic infection causes the death of the host. Even in such cases the causative organism may remain undetected because although it has set in motion a train of events which eventually kill the host, it has itself been killed and eliminated before the host died (Case 14, p. 285).

A cursory survey of the available literature (Baylis 1951, Hyman 1951, Noble 1931) produced a list of twenty-six species of parasitic worms and their larvae which infect Amphibia, and to this number many more can certainly be added. It is therefore no surprise to record that in nearly one half of the twenty-three cases presented here the causative organisms were trematodes, cestodes or nematodes. Five cases describe tumours, two of which were definitely malignant, while two others were benign but proved fatal because of their localisation. The remainder were due to bacterial or fungal infection.

The eight species reported on are :—

I. Salientia
Bufo calamita
Bufo bufo
Rana esculenta
Pipa pipa
Xenopus laevis

II. Urodela *Hynobius lichenatus*
Siren lacertina
Pseudotriton ruber schencki

Table 1 presents a synopsis of the case material in more detail. The case presentation follows the order of the Table. The preponderance of *Bufo* and *Xenopus* derives from the fact that these species were most abundantly available for investigation.

Synopsis of the cases presented.

Case No.	Species	Condition observed
		INFESTATION BY PARASITIC WORMS OR THEIR LARVAE.
1.	*Xenopus laevis*	Trematode in the gall bladder.
2.	*Siren lacertina*	Cercaria encysted in the liver.
3.	*Xenopus laevis*	Distome trematode in the Woffian duct.
4.	*Bufo bufo*	Multiple infestation of the intestine.
5.	*Xenopus laevis*	Trematode infestation of the lateral line system.
6.	*Xenopus laevis*	*Cephalochlamys namaquensis* in freshly imported specimens.
7.	*Xenopus laevis*	Unidentified intestinal parasites.
8.	*Pipa pipa*	Nematode infestation of the peritoneum.
9.	*Hynobius lichenatus*	Nematode infestation of the kidney.
10.	*Pseudotriton ruber schencki*	*Enchytraeae* under the *stratum corneum*.
		TUMOURS, BENIGN AND MALIGNANT.
11.	*Bufo calamita*	Pulmonary carcinoma.
12.	*Xenopus laevis*	Renal carcinoma.
13.	*Xenopus laevis*	Multiple subcutanous granulomata.
14.	*Xenopus laevis*	Pelvic fibroma.
15.	*Xenopus laevis*	Facial fibromata.
		CONDITIONS DUE TO INFLAMMATORY PROCESSES.
16.	*Bufo bufo*	Inflammatory granuloma of kidney.
17.	*Bufo bufo*	Miliary tuberculosis.
18.	*Xenopus laevis*	Renal tuberculosis.
19.	*Bufo bufo*	Renal inflammatory granuloma with heterotopic cartilage.
20.	*Rana esculenta*	Mesenteric thrombophlebitis.
		CONDITIONS DUE TO FUNGAL INFECTION
21.	*Bufo bufo*	Subcutaneous tumours.
22.	*Bufo bufo*	Fungal ulceration of the skin of the head.
23.	*Bufo bufo*	Fungal infection and cystic degeneration of the kidney.

INFESTATION BY PARASITIC WORMS OR THEIR LARVAE

Case Nos. 1–3. *Xenopus laevis* and *Siren lacertina*.

Parasitic worms and their larval stages are the greatest enemies of amphibians. Both pass part of their life cycle in the water and many amphibians become the intermediate hosts of cercariae or the permanent host of many kinds of worm. Amphibians reared under strict laboratory conditions may be free of these parasites but all imported animals are potentially infected and the infestation may show itself even after years of captivity if the animal survives. Since we do not import the snails which are, in many cases, indispensable intermediate hosts of these worms, we hope

they will not become permanently established in our tanks. Even if a high percentage of our animals are infected, many will survive because worm and host often live in symbiosis for a long time. The helminths shown in Figs. 1–3 were discovered accidentally in animals seemingly healthy, which were killed for purposes unconnected with this paper. It is remarkable that in spite of their relatively large size (one worm nearly filling the gall bladder, another seemingly obstructing the Wolffian duct) the animals displayed no symptoms of disease, neither did their tissue show any indication of a defensive reaction. This may seem surprising, but in these cases the host tissues could not have been irritated by the presence of the worm.

Case No. 4. *Bufo bufo*. Multiple infestation of the intestine.

Even a parasite harmless in small numbers may cause the death of the host if it becomes too abundant. *Nematotaenia dispar*, a common commensal of the jejunum of *B. bufo*, can reach a length of 1–3 cm. without causing much harm to the host, but a case was seen in which a cluster of these worms had caused intestinal obstruction in the upper jejunum of an adult male toad. The jejunum from the site of the obstruction to the rectum had become gangrenous, a condition which, naturally, the toad could not survive.

Another toad (Case 5) lived in captivity for three months without showing any signs of disease. It then refused food, became emaciated and died. The intestinal tract was found to be in a state of acute inflammation. It was unlikely that this should be caused by the numerous young of the common lung worm *Rhabdias bufonis* of the toad, for these are always present in the intestine of *Bufo bufo*. Eventually a different species of worm was found, apparently engaged in nipping off a piece of the mucous membrane (Fig. 4). Further investigation identified this worm as *Acanthocephalus ranae*, 2–3 mm. in length, commonly found in the intestine of frogs and toads. *A. ranae* has neither mouth nor digestive tract. It absorbs nutriment through its epidermis and attaches itself to the intestinal mucous membrane by means of its relatively large proboscis, which is covered with curved hooks. This proboscis is retractable and sections show that in retracting it the worm pulls out part of the mucous lining of the host's gut, from which apparently it cannot detach itself once the hooks have become anchored. The worm thus remains attached to the host, whether its proboscis is extruded or retracted. In one case four *Acanthocephalus* were found in an area of 1 sq. cm. Infestation by this worm, in addition to the other helminths commonly infesting *Bufo*, is more than the animals can bear, and the infection set up by the injury to the intestinal tract, as much as the inability to digest any food, causes death (Figs. 4 and 5).

Case No. 5. *Xenopus laevis*.

The condition mentioned under this case has been described before (Elkan & Murray, 1952). It has been included again because it is one of those rare cases where an intensive defensive host reaction against cercariae occurred. In the four specimens which eventually died from this infestation, the whole lateral line system, i.e. every neuromast patch was affected. The toads (*X. laevis*) were part of a large consignment received from Cape Town. The infection remained latent for at least a year. The four cases described

Fig. 1.—*Xenopus* Adult female. Gallbladder with parasitic worm. (Case 1.)

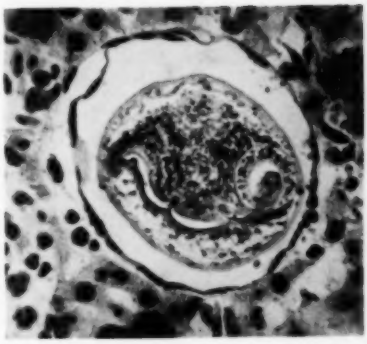


Fig. 2.—*Siren lacertina*. 10 cm. long specimen. Trematode encysted in liver. (Case 2.)

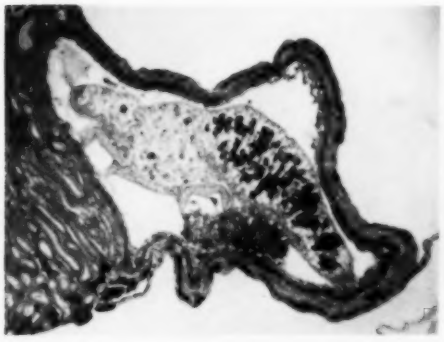


Fig. 3.—*Xenopus laevis*. Import. Kidney. Distome trematode in Wolffian duct. (Case 3.)

Fig. 4.—*Acanthocephalus ranae* in the small intestine of *Bufo bufo*. The worm has retracted the proboscis and pulled out a fold of the mucous lining of the toad's intestinal canal. (Case 5.)

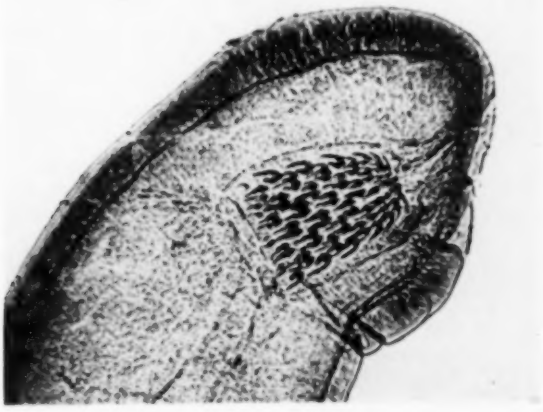
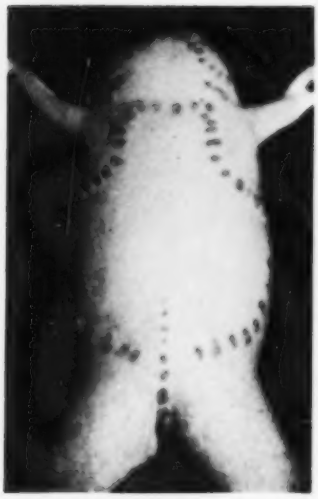
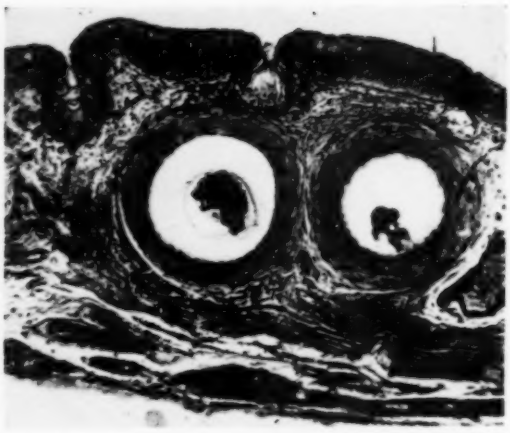
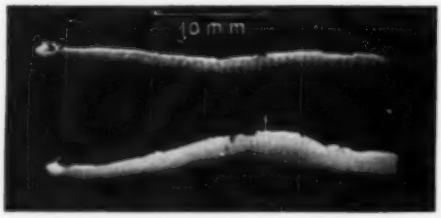


Fig. 5.—*Acanthocephalus ranae*. Proboscis retracted. Mayer's carmin. (Case 5.)

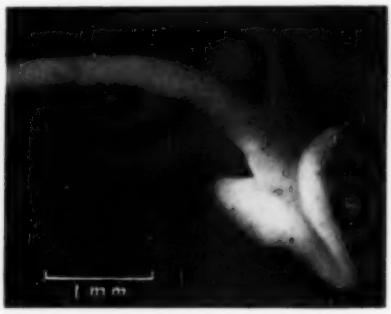




Figs. 6 & 7.—*Xenopus laevis*. Larval trematode infestation of dermis in region of lateral line system. (Case 5.)



Figs. 8 & 9.—*Cephalochlamys namaquensis*. Whole worms. (Case 6.)



Scolex

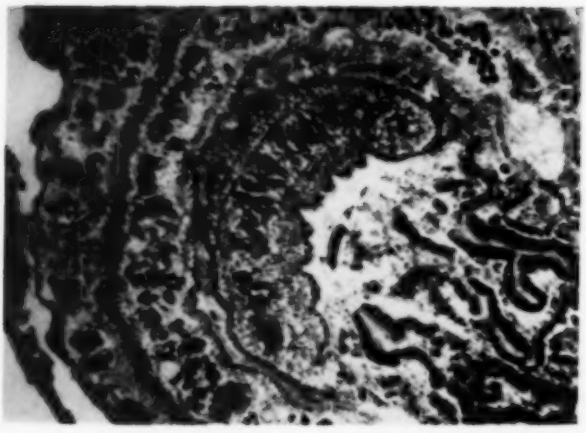


Fig. 10.—*Xenopus laevis*. Unidentified intestinal helminths. H & E. (Case 7.)

occurred at short intervals. No new cases have been observed since and it is not known whether this condition has ever been seen in South Africa. The affected specimens lost their equilibrium, stopped feeding and became pale, while an intensive melanosis occurred around the cercarial cysts. It must be assumed that even the strong defensive capsule produced by the host did not prevent the absorption of an exotoxin produced by the cercariae. Every affected toad died within a fortnight after the disease manifested itself (Figs. 6 and 7).

Case No. 6. *Cephalochlamys namaquensis* in *Xenopus laevis*.

This tapeworm of the family Dibothriocephalidae is occasionally present in specimens of *Xenopus* imported from South Africa. In a consignment of 210 toads, five produced complete worms ; in two others the segments only were recovered. Cohn, who first described this worm in 1906, found over 100 scolices in one toad. Those recovered from recent consignments were 36 mm. in length (against Cohn's 18 mm.) with sixty proglottids against his fifty maximal number. The worms are always extruded within twelve hours after the toads have received an injection of urinary extract for the purpose of a Pregnancy Test, irrespective of whether the test is positive or negative. It must be assumed that a constituent other than the gonadotrophin, probably the Brom-Phenol indicator, acts as a vermifuge. Recurrences of this infestation have not been observed among captive toads. The full life cycle of this worm is as yet unknown (Figs. 8 and 9).

Case No. 7. Unidentified helminths in *Xenopus laevis*.

A female specimen of *X. laevis* weighing 40 gm., which was kept with others in the laboratory, died. The small intestine was inflamed and the coils matted together by adhesions. Sections revealed the presence of a great number of intestinal worms, the identity of which it has as yet been impossible to establish (Fig. 10).

Case No. 8. *Pipa pipa* infested by nematodes.

The Surinam water toad is much more closely adapted to its environment than *Xenopus*, its related African form, and more difficult to keep in captivity. Occasionally autopsy reveals why freshly imported specimens die in spite of every care. The specimen shown here survived for a month but refused to feed, because of the presence of cysts containing nematode larvae in various stages of development along a large stretch of its small intestine. No mature worms were found and it has not been possible to identify the worms.

Better chances of keeping *Pipa* in captivity might occur if young specimens not yet infested with parasites could be imported (Figs. 11 and 12).

Case No. 9. *Hynobius lichenatus*. Renal infestation with nematodes.

Nematodes, although most frequently seen in the intestinal tract, are not confined to that area nor do they necessarily cause the death of the host. They are often found in the organs of animals thought to be healthy.

The specimen of *H. lichenatus* described here was caught and killed in Japan. It presented no outward signs of disease, yet the kidneys showed a heavy infestation with nematodes when sections were examined. It is

interesting to note that the worms (or their larvae—fixation was not sufficiently good to allow for exact typing) were only found in the renal collecting tubules, both proximal and distal convoluted tubules being free from parasites (Fig. 13). Assuming that the worms entered the renal system from the Wolffian duct, no anatomical obstacle would have prevented them to progress beyond the collecting ducts, and any concentration of electrolytes would rather become lower and lower the closer the worm approached Bowman's capsule. However, considering how closely the worms are packed in the collecting tubules, it must be assumed that the pH there was particularly suitable for their requirements. Sections of the kidney of an adult female *Xenopus* which showed no sign of disease other than an inability to react to injections of gonadotrophin, showed similar nematode larvae in Bowman's capsule and only there. It would be interesting to know if different nematode larvae, occurring in different hosts, have different habitat preferences and select to remain in a particular section of the nephron.

Case No. 10. *Pseudotriton ruber schencki* infested with *Enchytraea*.

Worms are not always the cause of amphibian death. A specimen of *Pseudotriton ruber schencki* imported from the U.S.A. by a German dealer, eventually arrived in England. On arrival it was not in very good condition ; it would not feed and died within a week. The presence of large numbers of worms in the oral cavity and under the stratum corneum of the skin seemed to explain the death of the salamander. On closer examination, however, the worms proved to be oligochaete annelids and these, having no piercing mouth organs, would be unable to force an entrance through the intact skin. The worms were eventually identified as being *Enchytraeae*, a species very commonly used as a food for small amphibians, particularly for urodeles. They probably gained entrance beneath the stratum corneum when this was being shed and were entirely unconnected with the death of the ' host ' (Fig. 14).

TUMOURS, MALIGNANT AND BENIGN

Case No. 11. *Bufo calamita*. Pulmonary carcinoma.

The specimen under observation was an adult female which had been kept in captivity for over a year. Eventually it refused to feed, became more and more emaciated, and died. Autopsy revealed the presence of white, firm nodules of 1–2 mm. diameter disseminated throughout both lungs. Sections showed an adenocarcinoma invading the alveoli and filling them more or less completely without, however, destroying the fundamental pulmonary structure (Fig. 15). The toad died probably more from inanition than from asphyxiation since large parts of the lung had not yet been invaded by the tumour.

Spastic paralysis of the hind legs, a symptom difficult to explain but one often observed in diseased frogs or toads, was also present in this case. In aquatic species like *Xenopus* this spastic paralysis often prevents the specimen from coming to the surface for air so that it drowns. Nothing abnormal in the brain or the spinal cord of these animals has so far been discovered. It may be that a neurotoxic factor is responsible.

Fig. 11.—*Pipa pipa*. Intestinal canal of adult male with nematode infection. (Case 8.)

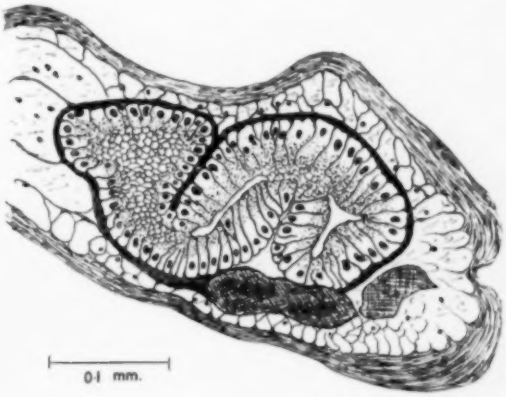


Fig. 12.—Nematode larva. From a cyst attached to the small intestine of a specimen of *Pipa pipa*. (Case 8.)

Fig. 13.—*Hynobius lichenatus*. Adult male. Kidney with nematodes in collecting tubules. (Case 9.)

Fig. 14.—*Pseudotriton ruber schencki*. Enchytraea under the stratum corneum of the epidermis. (Case 10.)

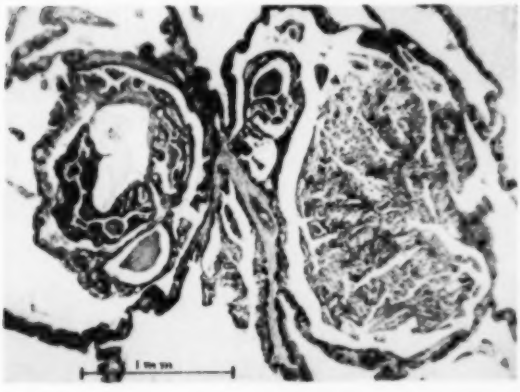


Fig. 15.—*Bufo calamita*. Pulmonary carcinoma. (Case 11.)

Fig. 16.—*Xenopus laevis*. Renal carcinoma. (Case 12.)

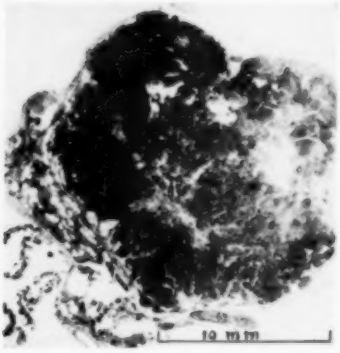


Fig. 17.—*Xenopus laevis*. Renal carcinoma. Compressed renal tissue on lower left. (Case 12.)

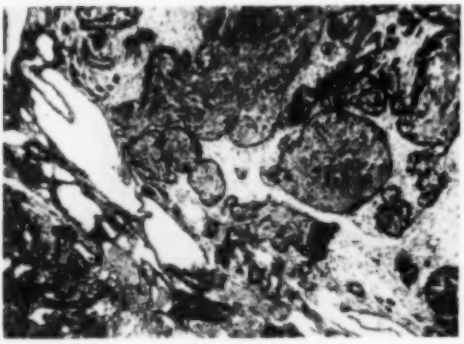


Fig. 18.—*Xenopus laevis*. Adult female. Renal carcinoma. Invasion of renal tubules × 40. (Case 12.)

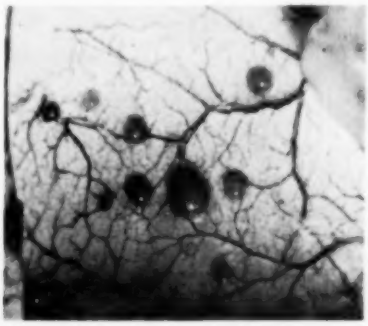


Fig. 19.—*Xenopus laevis*. Tumours on inner side of abdominal skin. Natural size. (Case 13.)

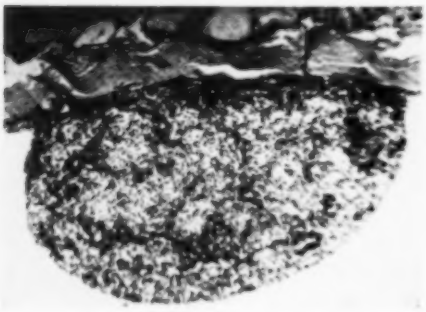


Fig. 20.—*Xenopus laevis*. Granuloma on inner aspect of dorsal skin × 30. (Case 13.)

Fig. 21.—*Xenopus laevis*. Normal urinary bladder, sagittal × 10 H.E. (Case 14.) Compare with Fig. 22

Case No. 12. *Xenopus laevis*. Renal carcinoma.

Renal carcinoma was discovered in an adult female of about 120 gm weight, received with many others from Cape Town. For the first six months the specimen behaved normally ; it then stopped feeding and its abdomen gradually increased beyond normal proportions. Since the animal was not likely to recover, it was killed with urethane.

When the abdomen of a normal, fully grown female *Xenopus* is opened the first organ to come into view is invariably the ovary. In this case the left oviduct presented, pushed forward by a tumour the size of a large hazelnut which was found to lie retroperitoneally in continuation with the left kidney. All the other intestines were accordingly displaced forward and to the right (Fig. 16).

Sections showed the tumour to be a typical renal adenocarcinoma (Figs. 17 and 18) which had compressed and destroyed most of the left kidney, the right kidney being normal. Higher magnification revealed the presence of nuclear inclusion bodies. The tumour stained well at the periphery while central parts, due probably to insufficient blood supply, showed signs of degeneration (Fig. 17).

Similar tumours occurring in *Rana pipiens* have been described by Lucké (1934, 1938 and 1952) and in some urodeles (Schlumberger & Lucké, 1948) but they have not previously been described as occuring in *Xenopus* and must be regarded as very rare. According to Lucké the batrachian renal adenocarcinoma is due to a virus which, if transferred to other amphibian species, produces cartilaginous and periosteal tumours analogous to a similar behaviour of the Rous sarcoma.

The rarity of these tumours in *Xenopus* makes further study of this interesting condition difficult. In the course of twenty years of daily supervision of a large colony of *Xenopus* only one other renal carcinoma was discovered in routine examination of kidneys of this species. The tumour had, in this case, started in the anterior pole of the kidney and produced a much more pronounced development of stroma than the first tumour seen in *Xenopus*. Within the meshes of this stroma the tumour itself showed the typical pictures of an adenocarcinoma with good differentiation. No inclusion bodies were seen in this case.

Case No. 13. *Xenopus laevis*. Subcutaneous granulomata.

In amphibians which have large subcutaneous lymph spaces it is possible to view the skin from both the external and the internal aspect. Such an inspection frequently discloses the presence of small, firm round tumours of 1–3 mm. diameter which are firmly adherent to the interior aspect of the dermis. Sections show these tumours to consist entirely of densely packed small round cells with very little cytoplasm. There is no stroma and no capillaries extend into the tumours. There is no degeneration at the centre of the tumours. Microorganisms could not be demonstrated. The nature of these tumours remains open to speculation (Figs. 19 and 20).

Case No. 14. *Xenopus laevis*. Pelvic tumour.

The toad, a large adult female, died " from natural causes " without showing

any external signs or symptoms of disease. Autopsy revealed, as the only abnormality present, a tumour of 8 mm. diameter, situated close to the urinary bladder but not in continuity with it (Fig. 22). The tumour was firm and pale and was attached to the pelvic wall.

The specimen was sectioned whole and the following picture was obtained : The tumour itself had hardly any cellular structure but consisted of concentric layers of badly staining tissue with some nuclei in the periphery, none at the centre. Such a tumour might very well have arisen as a defence against an encysting cercaria. Encysting trematode larvae are not uncommonly seen in *Xenopus* (Elkan & Murray 1952). They can lead to a strong host reaction with the formation of a dense fibrous capsule. If eventually the cercaria dies, the capsule remains as a firm round tumour which does not reabsorb itself. The toad would probably have survived this if the tumour had not, in some way, obstructed the bladder. The mechanism of how this occurred is not easy to understand since in amphibians the bladder is a separate diverticulum of the cloaca and the flow of urine should not be obstructed even if the bladder was out of action. However, the fact remains that in these sections the bladder looks severely hypertrophic and that the specimen died. Comparison of the normal and the diseased bladder tells what happened in this case (Figs. 21 and 22).

Case No. 15. *Xenopus laevis* D. Facial tumours.

A large adult female was observed with tumours developing in the region of the external nares (Fig. 23). It was first thought that these tumours might have developed as a result of an injury or an abrasion of the skin which commonly occurs in frogs which try to escape from their containers. The tumours in this case were however not at the extreme tip of the head but appeared on both sides in the region of the nasal apertures. Also, the toad was not a fresh import and no such injuries were observed in the other toads sharing the cage.

Since the tumours did not look malignant the animal was not destroyed. It continued to feed for nine months when the tumours showed signs of regression (Fig. 24). It was hoped that the lesion might now disappear and heal but the animal, at this stage, stopped feeding and died, apparently from inanition. The tumours had, by that time completely disappeared and sections showed nothing but a widespread destruction of the maxillary region of the skull. This would explain the animal's inability to feed. The condition was otherwise not malignant and all other organs looked perfectly healthy. The case confirms that mature amphibians have poor healing powers. A defect of the skin invariably develops into an ulcer which, if it heals at all, takes a very long time to do so.

CONDITIONS DUE TO INFLAMMATORY PROCESSES

Case No. 16. *Bufo bufo.* Renal inflammatory tumour.

This male adult toad was part of a colony kept for the purpose of Pregnancy Tests. It had been injected an unspecified number of times with urinary extracts which were not sterile. It is possible, indeed probable, that the

Fig. 22.—*Xenopus laevis*. Transverse section through pelvis. Urinary bladder grossly hypertrophic due to obstruction caused by a pelvic tumour. Van Gieson. × 10. (Case 14.)

Fig. 23.—*Xenopus laevis* with facial tumours. (Case 15.)

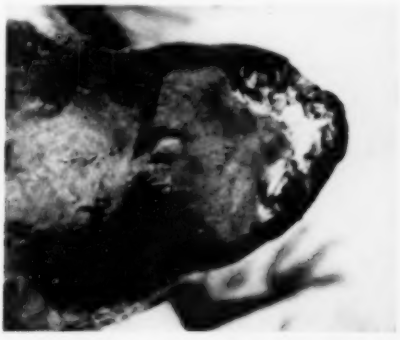


Fig. 24.—*Xenopus laevis*. Ulceration of maxilla after degeneration of tumour. (Case 15.)

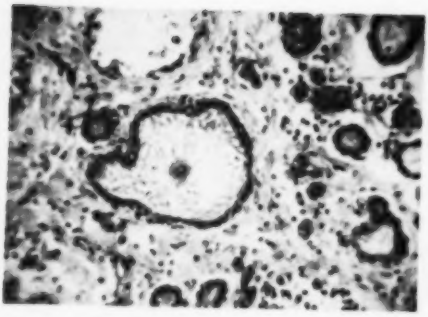


Fig. 25.—*Bufo bufo.* Kidney. Inflammatory tumour, destroying the nephrons but not the ciliated tubules. (Case 16.)

Fig. 26.—*Bufo bufo.* Adult male. Died spontaneously. Liver. Miliary tuberculosis. (Case 17.)

Fig. 27.—*Bufo bufo.* Adult male. Died spontaneously. Liver, inferior surface Miliary tuberculosis. (Case 17.)

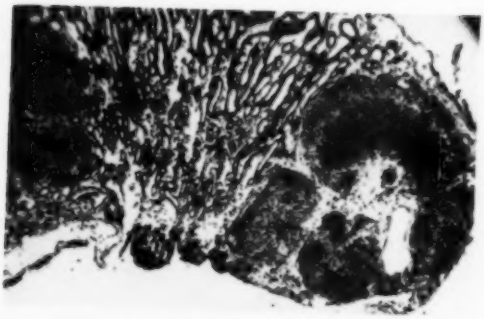


Fig. 28.—*Bufo bufo.* Adult male. Died spontaneously. Miliary tb. of kidney. H & E. (Case 17.)

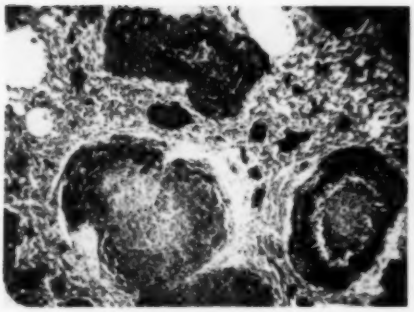


Fig. 29.—*Bufo bufo.* Adult male. Died spontaneously. Miliary tb. in the spleen. H & E. (Case 17.)

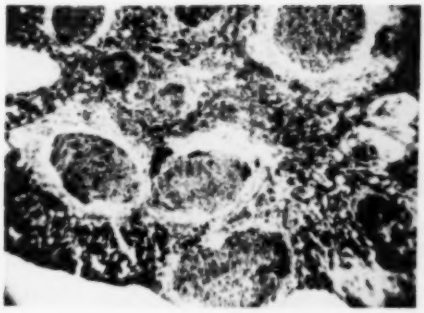


Fig. 30.—*Bufo bufo.* Adult male. Died spontaneously. Miliary tb. in the liver. (Case 17.)

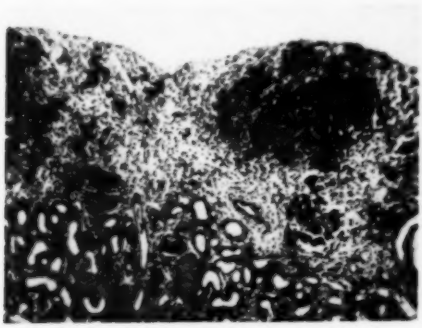


Fig. 31.—*Xenopus laevis.* Adult female. Kidney. Infection with acid fast bacilli. H & E. (Case 18.)

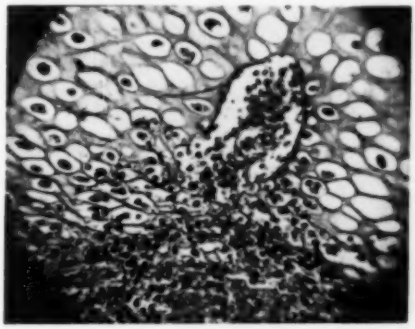


Fig. 32.—*Bufo bufo.* Adult male. Abdominal tumour (inflammatory) with central formation of cartilage. v. Gieson. (Case 19.)

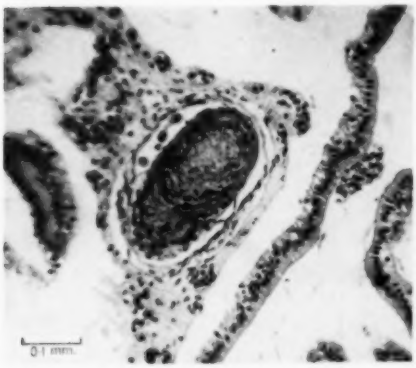


Fig. 33.—*Rana esculenta.* Small intestine. Thrombophlebitis (Case 20.)

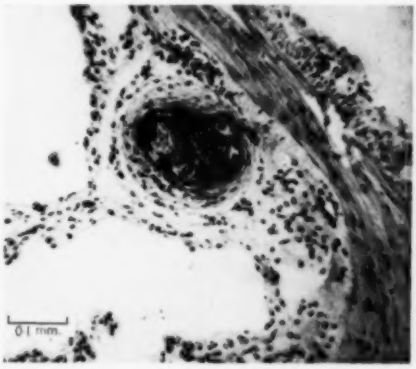


Fig. 34.—*Rana esculenta.* Small intestine. Thrombophlebitis. (Case 20.)

Fig. 35. *Bufo bufo.* Adult. Caught at Ambleside 8/1958 with two subcutaneous tumours on the back. (Case 21.)

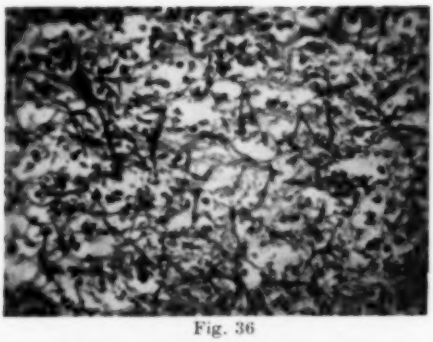


Fig. 36

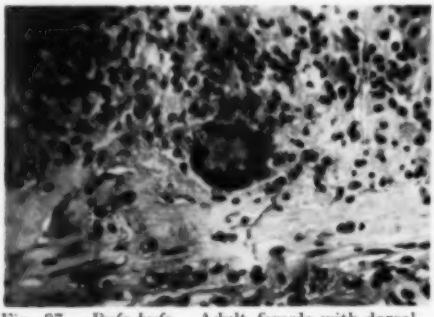


Fig. 37.—*Bufo bufo.* Adult female with dorsal subcutaneous tumours. Giant cells in the periphery of the tumour. (Case 22.)

Fig. 38

Fig. 39.—*Bufo bufo.* Adult male. Fungal ulceration of the head. PAS-Htxln.-Tartrazine. (Case 22.)

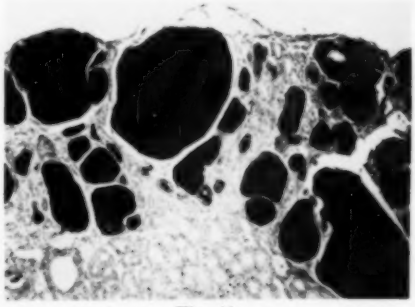


Fig. 40

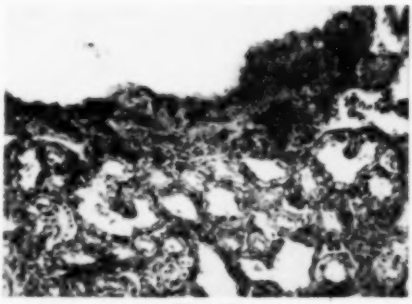


Fig. 41

Fig. 36.—*Bufo bufo.* Adult female from Lake District, summer 1958. Section through dorsal, subcutaneous tumours showing fungal mycelium. PAS-Htxln. (Case 21.)

Fig. 38.—*Bufo bufo.* Fungus infection of head. IV/1959. (Case 22.)

Fig. 40.—*Bufo bufo.* Cystic degeneration of kidney PAS.-Htx.-Tartraz. (Case 23.)

Fig. 41.—*Bufo bufo.* Fungal mycelium on the renal surface. PAS.-Htxln. (Case 23.)

inflammatory renal tumour was not a spontaneous disease but artificially induced.

The interest of the case lies in the fact that the inflammatory cells destroyed all the segments of the nephrons with the exception of the ciliated parts and the nephrostomes. The ciliated parts—probably because they became obstructed—were in many cases seen to be quite abnormally dilated (Fig. 25). No explanation for their resistance to the toxins which destroyed the convoluted tubules can be offered at present.

Case No. 17. Miliary tuberculosis in *Bufo bufo*.

An adult male, obtained from a dealer in the spring of 1959, was kept in a suitable tank, together with other toads of the same species but not used for any experiments until July 1959, when it died spontaneously.

Autopsy showed the liver to be enlarged two to three times both in transverse and longitudinal direction. A great number of white opaque tumours of 0·5–1 mm. in size were seen on the surface of the liver and other intestinal organs (Figs. 26 and 27).

Sections showed these tumours to consist of monocytes and in the peripheral parts of the tumours numerous acid-fast bacteria were seen. The cells in the centre of the tumours were less well defined but complete caseation had not occurred. Giant cells were found at the periphery of some of the liver tumours.

Tubercles of this description were found in the following organs : Liver (Fig. 30) ; Kidney (Fig. 28) ; Lungs ; Small intestine ; Fat-body ; Spleen (Fig. 29) ; Testis. Schwabacher (1959) has shown that acid-fast bacilli may cause skin disease in *Xenopus* and a case of tuberculosis in *Rana temporaria* was described by Lichtenstein in 1920. As far as I am aware this condition has not been recorded in *Bufo*. It is to be noted that this specimen presented an isolated case occurring in a tank containing about twenty-five other toads, and that all its major intestinal organs could become affected to this degree before it died. No tubercles were seen in any but the visceral organs.

A second case of miliary tuberculosis has since been seen in a specimen of *B. bufo*. All abdominal viscera, particularly the fat-body, the testes and the kidneys were involved, but neither the liver nor the lungs were affected.

Case No. 18. Tuberculosis in *Xenopus laevis*.

A large adult female kept with many others in a tank for the purpose of Pregnancy Tests was found to suffer from hydrops of the subcutaneous lymph sacs of the right leg. The fluid was aspirated and subjected to bacteriological examination. It was found to be sterile. The lymph sacs refilled within twenty-four hours. Since it has been found that hydropic animals never recover, and since an obscure infection presents a danger to other toads in the same tank, the animal was killed with urethane. Dissection revealed a tumour of irregular extension, approximately 1×2 cm. large, occupying the coccygeal region. The tumour was firmly adherent to the surrounding tissues from which it could not be separated. The left kidney was the seat of a round tumour of 5 mm. diameter embedded in the parenchyma. While the histological picture obtained from the coccygeal tumour was that of unspecific pyogenic inflammation, the kidney showed a large typical tubercle containing

very numerous acid-fast bacilli in the periphery and showing caseation at the centre (Fig. 31). The location of the subcutaneous tumour and the fact that this toad had been used for Pregnancy Tests make it seem possible that the infection was artificially introduced into the dorsal lymph sac. So far this is the only case of this kind that has been observed.

Case No. 19. *Bufo bufo*. Renal inflammatory tumour.

In a routine autopsy of common toads, kept for Pregnancy Tests, this animal was found to have a relatively large tumour (10×12 mm.) replacing the left kidney. The small intestine looked hyperaemic and there was some sanguinous fluid in the peritoneal cavity. The tumour, on sectioning, proved to be a large mass of inflammatory tissue and might not have attracted much attention had it not been for the presence of an island of cartilage in the centre. The tumour had developed from the anterior (ventral) aspect of the kidney where normally no cartilage would occur, and it was not continuous with any part of the skeleton. This tissue must therefore be regarded as heterotopic cartilage which developed from fibroblasts or other mesenchymal cells which were abundant in the tumour (Fig. 32). The development of this cartilage must obviously have taken some time and it could be seen that in the process the left kidney had been almost completely destroyed. The power of the toad to survive a condition of this severity for so long is remarkable.

Case No. 20. *Rana esculenta*. Thrombosis of intestinal vessels.

This specimen of the edible frog had been kept in captivity for three to four months when it lost its appetite and became very emaciated. It was killed but the autopsy revealed no gross pathology apart from a completely empty intestinal canal. Sections through the gut however showed an unexpected condition which had not been observed before in Salientia. Many of the larger blood vessels—probably veins—were seen obstructed by thrombi in the process of organization. The obstructed vessels were probably veins because the walls were thin and the animal would have died from intestinal gangrene if the arteries had been thrombosed. No obvious cause for this mesenteric thrombosis could be discovered and it may be debatable whether or not this case should have been included among the inflammatory conditions. A mesenteric phlebitis however seemed the most likely condition to explain this picture (Figs. 33 and 34).

FUNGAL INFECTION IN *Bufo bufo*

Case Nos. 21–23. *Bufo bufo*. Epidermal and renal fungal infection.

The first of the three specimens described here was received through the kindness of Mr S. Nield of the Freshwater Biological Association at Ambleside, who caught it in that neighbourhood and noticed that it had two tumours of approximately equal size on its back (Fig. 35). Since the animal seemed otherwise in good condition and fed well, it was kept under observation. It continued in good health for a year. It then began to refuse food, lost weight and eventually died spontaneously.

The tumours were found to lie subcutaneously and consisted of large,

centrally necrotic masses surrounded with small-cell infiltration and large giant cells (Fig. 37). In all parts of the tumours, but particularly in the centre, a dense fungal network could be seen. The fungus stained badly with the usual reagents but could be very well demonstrated by means of the periodic acid Schiff technique. Only mycelium and no fruiting bodies were seen (Fig. 36). Examination of the internal organs of the toad revealed nothing abnormal and it was assumed that the toad had been poisoned by an exotoxin secreted by the fungus.

A second case of fungoid infection in *Bufo* occurred in a colony of toads kept for Pregnancy Tests. Only one animal was affected ; its origin is not known. This time the condition presented itself as an irregular swelling, almost like a cap, which gradually covered the whole of the head, spreading from the mid-frontal region towards the eyes and the nostrils (Fig. 38). The toad was killed when it finally refused to feed. Close examination of the " cap " showed this to consist of a large mass of coagulated fibrin and dermal detritus covering an area where the skin was completely ulcerated. In various parts of this mass could be seen the mycelium of a fungus closely resembling the one previously described, with the only exception that in this case giant cells were absent. Fruiting bodies were again not seen (Fig. 39).

The third case in this series presents a different aspect. The toad in question died spontaneously and on autopsy the left kidney looked enlarged and paler than usual. Sections revealed the distal convoluted tubules to be excessively dilated and filled with a strongly PAS positive substance (Fig. 40). On the renal surface and deeply embedded in the parenchyma, a fungal mycelium, again closely resembling that seen before, was found. But whereas in the first two cases this fungus had apparently caused a widespread destruction and ulceration of the affected tissues, it was in this case limited to a narrow zone on the renal surface (Fig. 41). Many collecting and convoluted tubules in the deeper parts of the kidney looked quite normal even when lying in the immediate neighbourhood of fungal threads. The extreme cystic dilatation of the proximal convoluted tubules is thought to be due to their obstruction in the more distal parts of the nephrons affected.

The typing of the fungus concerned was made difficult by the absence of fruiting hyphae in all these cases. The material has been transferred to Mr P. Austwick of the Central Veterinary Laboratory of the Ministry of Agriculture, who will report on it in more detail when his investigations are concluded.

ACKNOWLEDGMENTS

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Finally I should like to thank Professor K. Takewaki of Tokio University most cordially for repeated supplies of Japanese urodeles.

SUMMARY

Observations made during the autopsy and histological investigation of amphibians show that their death is more commonly due to parasites than to other causes. The material presented consists of ten cases of helminth infestation, five cases of benign or malignant tumours, four cases of inflammatory processes and three cases of fungal infection.

ADDENDUM

While this paper was in the press another remarkable case has been observed in a male specimen of *Triturus vulgaris* which might well find a place

Fig. 42.—*Triturus vulgaris* L. Male. Rupture of left lateral thoracic wall with herniation of stomach.

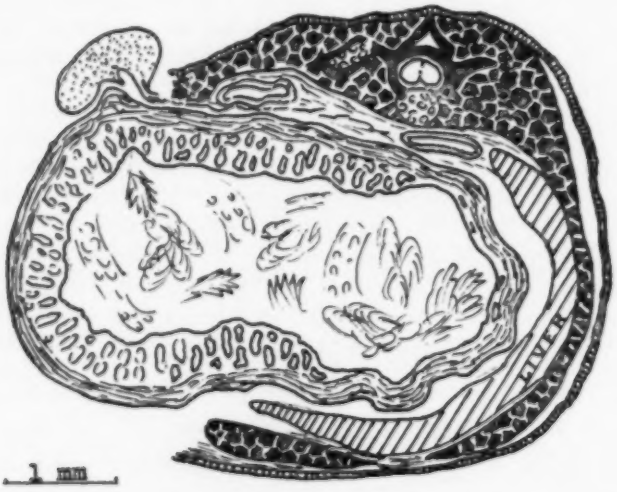

Fig 43.—*Triturus vulgaris* L. Adult male. Rupture of left thoracic wall and herniation of part of stomach and fat-body. Stomach filled with fermenting vegetable debris.

in this review. The animal was one of several common newts kept in an aqua/terrarium in a room at ±22°C. From October onwards the animals

were not fed and remained hidden under moss and bark. In December one male was seen crawling about with a tumour of 6 mm. diameter on the left side of the thorax, just behind the insertion of the left fore leg. The animal was lively and by no means moribund, but since, affected by a tumour of this size, it was unlikely to survive, it was killed with Urethane and the thorax sectioned. It could then be seen that the " tumour " was, in fact, the stomach which had erupted through the left lateral body wall. The stomach itself was filled with vegetable debris, a kind of food not normally accepted by any amphibian. The abnormal food fermenting in the stomach, inflated the organ to such an extent that it eventually burst the wall of the thorax. Why this particular newt fed on all this vegetable matter while the others, of the same species and in the same cage, did not, remains inexplicable.

In " Pathologie der Laboratoriumstiere " a textbook by P. Cohrs, H. Jaffe, H. Meesen and 57 contributors, which came under review after the completion of this paper, only eleven of the 1,602 pages in this work are devoted to amphibian pathology, sixteen to fish and five to reptiles, which emphasizes how little is known of the pathology of the lower vertebrates.

REFERENCES

Baylis, H. A. (1929). Some parasitic nematodes from the Uluguru and Usambara Mountains, Tanganyika Territory. *Ann. Mag. nat. Hist.* (10) **4** : 372.

Baylis, H. A. (1932) in Parker, H. W. Scientific results of the Cambridge Expedition to the East African Lakes, 1930–31. V. Reptiles & Amphibians. *J. Linn. Soc.* (Zool.) **38** : 216.

Baylis, H. A. (1934). Miscellaneous notes on parasitic worms. *Ann. Mag. nat. Hist.* (10) **13** : 223–228.

Baylis, H. A. (1951). The parasitic worms of British reptiles and Amphibia in Smith, M. *The British amphibians and reptiles.* London : Collins.

Bigler, J. A. & Killingsworth, W. (1949). Cartilage in the kidney. *Arch. Pathol.* **47** : 487.

Chait, L. (1938). On some parasitic worms found in *Xenopus laevis*, the South African claw footed toad. Thesis (M.Sc.) Capetown. Typescript. (Not seen.)

Cohrs, P., Jaffe, R. & Meessen, H. (1858) *Pathologie der Laboratoriumstiere.* 2 vols. Berlin : Springer.

Cowdry, E. V. (1955). *Cancer cells.* London : W. B. Saunders.

Dawes, B. (1946). *The trematodes.* Cambridge University Press.

Elkan, E. & Murray, R. W. (1952). A larval trematode infection of the lateral line system of the toad *Xenopus laevis*. *Proc. zool. Soc. Lond.* **122** : 121–126.

Gilchrist, D. F. (1918). The life history of *Distoma luteum* n. sp. with notes on some cercariae and rediae found in South Africa. *Parasitology* **10** : 311–319.

Grobbelaar, C. S. (1922). Some trematodes in South African anurans and their relationships and distribution of their hosts. *Trans. Roy. Soc. S. Afr.* **10** : 191–200.

Hyman, L. H. (1951). *The invertebrates*, vols. 2 & 3. New York : MacGraw-Hill.

Loveridge, A. (1953). Zoological results of a fifth expedition to East Africa. IV. Amphibians from Nyasaland and Tete. *Bull. Mus. comp. Zool. Harv.* **110** : 232–406.

Lucké, B. (1934). A neoplastic disease of the kidney of the frog *Rana pipiens*. *Amer. J. Cancer* **20** : 352–379.

Lucké, B. (1938). Carcinoma in the leopard frog. Its probable causation by a virus. *J. exp. Med.* **68** : 457–467.

Lucké, B. (1952). Kidney carcinoma in the leopard frog. A virus tumour. *Ann. N. Y. Acad. Sci.* **54** : 1093–1109.

Nicholson, G. W. (1922). Studies on tumour formation. III. Tissue malformations. Anomalies of position and of blending. *Guy's Hosp. Rep.* **72** : 333.

NIGRELLI, R. F. & MARAVENTANO, L. W. (1944). Pericarditis in *Xenopus laevis* caused by *Diplostomulum xenopi* sp. nov., a larval strigeid. *J. Parasit.* **30** : 184–190.

NOBLE, K. (1931). *The biology of the amphibians.* McGraw-Hill N.Y. re-edited Dover Publ. 1954 cf. for older literature.

ORTLEPP, R. J. (1926). On a collection of helminths from a South African Farm. *J. Helminth* **4** : 127–142.

PARKER, H. W. (1932). Scientific results of the Cambridge Expedition to the East African Lakes 1930/31. No. 5. Reptiles and amphibians. *J. Linn. Soc.* (Zool.) **38** : 215–216.

PRICE, E. (1943). A new trematode of the genus *Polystoma* from *Xenopus laevis* Daud. *Proc. Helminth. Wash.* **10** : 83–85.

SCHLUMBERGER, H. G. & LUCKÉ, B. (1948). Tumours of fishes, amphibians and reptiles. *Cancer Research* (12) **8** : 657–754.

SCHWABACHER, H. (1959). A strain of mycobacterium isolated from skin lesions of a cold blooded animal, *Xenopus laevis*, and its relation to atypical acid-fast bacilli occurring in man. *J. Hygiene* **57** : 57–67, cf. for older literature.

SOUTHWELL, T. A. & KIRSHNER, A. (1937). On some parasitic worms found in *Xenopus laevis*, the South African claw footed toad. *Ann. Trop. Med. Parasit.* **31** : 245–265.

WILLIS, R. A. (1958). *The borderland of embryology and pathology* London : Butterworth.

WORDEN, A. N., & LANE-PETTER, W. (ed.) (1957) *The UFAW handbook on the care and management of laboratory animals*, 2nd. ed.

REPORT OF THE SOCIETY'S PATHOLOGIST FOR THE YEAR 1958

BY

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[Accepted 9th February 1960]

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GENERAL

In the last report, a review was given of events occurring in the twelve months since the opening of the new Hospital and Pathology Laboratories. It had there been shown that, since the provision of the new facilities, deaths from infectious and other preventible causes had declined sharply. In the year now under review it is satisfactory to report that the improved position was maintained in spite of exceptionally severe winter weather which lasted well into April. The deaths which occurred during the four quarters and totals are given in Table I in which figures given in brackets refer to acclimatised

TABLE I

Deaths occurring during the year 1958.

	1st Qtr.	2nd Qtr.	3rd Qtr.	4th Qtr.	TOTAL
Mammals	42	33	44	68	187(140)
Birds	75	66	74	85	300(232)
Reptiles, etc.	48	44	58	150	230 (84)
Batrachians					46 (12)
TOTAL	165	143	176	303	763(468)

Figures in brackets refer to the deaths of animals that have been more than six months in the Gardens.

animals that is animals which had been resident in the Regent's Park Gardens for more than six months. Total deaths at 763 compare with a figure of 798 for 1957 and 944 for 1956. Table 2 gives the deaths from 1954 to 1958 inclusive together with the total population and the death rate expressed as a percentage of population. As usual a disproportionate number of deaths were those of unacclimatized animals which had spent less than six months in the Gardens. The proportion of these to the total is no less than 38 per cent.

TABLE 2

Deaths for the whole year and four preceding years.

Year	Mammalia	Aves	Reptilia	TOTAL	Total Stock	Percentage of population
1954	405	369	282	1056	3256	33
1955	256	556	352	1164	3084	38
1956	183	406	351	944	3084	31
1957	162	352	284	798	2991	27
1958	192	310	282	784	2914	23

The analysis of the causes of death amongst the main classes of animals is given in Table 3.

TABLE 3

Analysis of the causes of death amongst the main Classes

	Mammalia	Aves	Reptilia	Batrachia	TOTAL
Senility	4 (4)	13(11)	0 (0)	0(0)	17(15)
Inanition	0 (0)	2 (2)	36 (3)	0(0)	38 (5)
Injury, etc.	34(22)	30(19)	9 (7)	5(5)	78(53)
Specific Diseases ..	7 (1)	6 (4)	0 (0)	0(0)	13 (5)
Septicaemia	9 (8)	9 (6)	10 (8)	0(0)	28(22)
Tuberculosis	15(14)	15(15)	1 (1)	0(0)	31(30)
Mycosis	5 (4)	9 (7)	0 (0)	1(1)	15(12)
Parasitic	1 (1)	2 (1)	9 (5)	1(1)	13 (8)
Circulatory	2 (0)	12(12)	0 (0)	0(0)	14(12)
Alimentary	46(34)	90(69)	20(15)	7(3)	163(121)
Respiratory	30(28)	57(50)	59(34)	3(2)	149(94)
Urinary	2 (2)	30(16)	11 (6)	0(0)	43(24)
Generative	3 (1)	7 (7)	5 (1)	0(0)	15 (9)
Locomotor	0 (0)	0 (0)	0 (0)	0(0)	0 (0)
Nervous	3 (2)	4 (3)	0 (0)	0(0)	7 (5)
Endocrine	0 (0)	0 (0)	0 (0)	0(0)	0 (0)
Skin	0 (0)	0 (0)	0 (0)	0(0)	0 (0)
Metabolism, etc. ..	3 (3)	3 (2)	0 (0)	0(0)	6 (5)
Neoplasms, etc.	4 (3)	0 (0)	0 (0)	0(0)	4 (3)
Other causes	19(13)	11 (8)	70 (4)	29(0)	129(25)
TOTAL	187(140)	300(232)	230(84)	46(12)	763(468)

Figures in brackets are of deaths of animals resident in the Gardens for six months or over.

At the beginning of the year the old system of recording autopsies on printed Kalamazoo ledger sheets was abolished and a system of punch cards was adopted. With the new system an entire post mortem record can usually be included on a single card of 8 ins. by 5 ins. and this gives also a punched break-down of causes of death, infecting parasites, the house or station from

which the animal came and the clinical data from the Hospital records. It is now possible with some ease to prepare tables giving a wide variety of statistical data. The cards are filed by species and all cards relating to each species will, therefore, come to be filed together.

These cards are being cross-referenced to two collections which should be of value for reference purposes. These are first, a library of histological blocks secondly one of coloured microfilms. With the staff available it is not possible to make exhaustive histo-pathological examinations. In order, therefore, not to lose material that might be valuable in the future, such material from fresh normal organs, or from organs showing pathological changes is being fixed and stored in paraffin blocks for reference purposes. In addition, the laboratory was equipped early in the year with photographic apparatus suitable for copying, macro- and microphotography, and virtually all cases of any interest are being recorded on colour transparencies.

In this way, when it is not possible to make a fundamental study of an interesting case the material and records are being preserved so that in the future such a study could be made.

DIAGNOSES

Tables 4 and 5 show the number of examinations of specimens examined during the year for diagnostic purposes together with the positive results.

Owing to a number of losses from tuberculosis which occurred early in the year amongst the monkeys, a bacteriological survey was made of all monkeys in the Monkey House in order to detect infected animals. Stools from sixty-eight primates were examined, eight of which were found to be infected with acid-fast bacilli. The method used was to concentrate as much faeces as possible by incubating for 24 hours with anti-formin, and with tri-sodium phosphate for culture purposes. Most of the faeces is digested in this manner and the residue in centrifuged, smears are stained with Ziehl Neelsen stain and cultures are made on a modified Dubos medium and on Loewenstein's medium. This method gives quicker results than are obtained by animal inoculations. The results also appear to be more reliable, although difficulties are experienced in differentiating bovine from human type bacilli. However, even some idea of this can be obtained by making cultures on both glycerine and non-glycerine containing media to select the eugonic and the dysgonic strains. All cases discovered during this survey proved to be of bovine type.

Owing to the heavy losses of snakes which occurred in 1957, and following the work described in the previous report, all snakes in the Reptile House were surveyed for infection with helminths and with amoeba. To detect helminths direct stool examinations were made. To detect amoeba stool samples were seeded on suitable culture media as advised by Dr Neal of the Wellcome Institute. This work was started in 1957 and some account was given in the previous report. The final figures, which include those given in 1957, show that ninety-four samples of faeces were examined from seventy-one snakes of which three were shown to be positive for amoeba, seventeen positive for helminths.

TABLE 4

The infecting parasites identified in 305 clinical specimens from living animals amongst the main Orders of Mammalia.

	1	2	3	4	5	6	7	8	9	10	TOTAL
Cocci	3	0	2	0	0	0	0	0	0	3	8
Corynebacterium	1	0	0	0	0	0	0	0	0	0	1
Acid Fast	22	0	2	0	0	0	2	0	0	0	26
Pasteurella	0	0	0	0	0	0	0	0	0	0	0
Salmonella	0	0	4	0	1	0	1	0	0	3	9
Shigella	9	0	0	0	0	0	0	0	0	0	9
Coliforms, etc.	3	0	0	0	0	0	2	0	0	0	5
Brucella	0	0	0	0	0	0	0	0	0	0	0
Anaerobes	0	0	0	0	1	0	0	0	0	2	3
Spirochaetes	0	0	0	0	0	0	0	0	0	0	0
Actinomyces	1	0	0	0	0	0	0	0	1	0	2
Fungi	0	0	0	0	0	0	0	1	0	1	2
Viruses	0	0	0	0	0	0	0	0	0	0	0
Rickettsia and other organisms not specified	0	0	0	0	0	0	0	0	0	2	2
Cestodes	0	0	9	0	0	0	0	0	0	0	9
Nematodes	3	0	39	0	0	0	2	0	0	0	44
Filaria	0	0	0	0	0	0	0	0	0	0	0
Trematodes	0	0	0	0	0	0	0	0	0	0	0
Other Worms	0	0	0	0	0	0	0	0	0	0	0
Sporozoa, etc.	0	0	0	0	0	0	0	0	0	0	0
Trypanosomes	0	0	0	0	0	0	0	0	0	0	0
Amoeba	1	0	0	0	0	0	0	0	0	0	1
Coccidia	0	0	0	0	2	0	0	0	0	0	2
Balantidium	0	0	0	0	0	0	0	0	0	0	0
Other Protozoa	0	0	0	0	0	0	0	0	0	0	0
Mange Mites	0	0	0	0	1	0	0	0	0	0	1
Ticks and Lice	0	0	0	0	0	0	0	0	0	0	0
Other Ecto-parasites	0	0	0	0	0	0	0	0	0	0	0
TOTAL	43	0	56	0	5	0	7	1	1	11	124

Column 1. Primates ; 2. Insectivora ; 3. Carnivora ; 4. Pinnipedia ; 5. Rodentia and Lagomorpha; 6. Perissodactyla ; 7. Artiodactyla ; 8. Edentata ; 9. Marsupialia ; 10. Other Orders.

TABLE 5

The results of bacteriological, parasitological and biochemical tests on living animals.

	Positive	Negative	Pending	TOTAL
Mammals	121	197	—	318
Birds	18	70	—	88
Reptiles	23	57	—	80
TOTAL	162	324	—	486

AUTOPSIES

Autopsy findings are summarized in Tables 6, 7 and 8. It is of some interest to compare the cause of death for acclimatized and unacclimatized animals. Deaths in newly imported animals were very high as a result of respiratory infections ; it is also to be noted that there was a high death rate amongst the birds from nephritis. This was partly due to the high incidence of nephritis in humming birds which do not normally survive long. It is possible that these birds are rather old when caught and thus succumb easily to disease of the kidneys.

TABLE 6

Analysis of causes of death amongst the main Orders of Mammalia.

	1	2	3	4	5	6	7	8	9	10	TOTAL
Senility	0	0	3	0	1	0	0	0	0	0	4
Inanition	0	0	0	0	0	0	0	0	0	0	0
Injury, etc.	3	3	6	1	8	0	9	0	4	0	34
Specific Dis.	0	0	7	0	0	0	0	0	0	0	7
Septicaemia	1	1	1	0	1	0	4	0	1	0	9
Tuberculosis	6	0	4	0	1	0	4	0	0	0	15
Mycosis	1	0	0	0	0	0	1	0	3	0	5
Parasitic	0	0	0	0	0	0	0	0	1	0	1
Circulatory	1	0	1	0	0	0	0	0	0	0	2
Alimentary	4	4	10	0	23	0	2	0	3	0	46
Respiratory	5	1	6	1	7	0	8	0	2	0	30
Urinary	1	0	0	0	0	0	0	0	1	0	2
Generative	0	0	0	0	0	0	1	0	2	0	3
Locomotor	0	0	0	0	0	0	0	0	0	0	0
Nervous	2	0	1	0	0	0	0	0	0	0	3
Endocrine	0	0	0	0	0	0	0	0	0	0	0
Skin	0	0	0	0	0	0	0	0	0	0	0
Metabolism	1	0	0	0	2	0	0	0	0	0	3
Neoplasms, etc.	1	0	1	0	1	0	1	0	0	0	4
Other causes	3	1	1	0	13	0	0	1	0	0	19
TOTAL	29	10	41	2	57	0	30	1	17	0	187

Column.	1. Primates	29 (of which 3 under 6 months in collection).
,,	2. Insectivora including *Tupaia*	10 (5 under 6 months in collection).
,,	3. Carnivora	41 (17 under 6 months in collection).
,,	4. Pinnipedia	2
,,	5. Rodentia and Lagomorpha	57 (12 under 6 months in collection).
,,	6. Perissodactyla	0
,,	7. Artiodactyla	30 (5 under 6 months in collection).
,,	8. Edentata	1 (1 under 6 months in collection).
,,	9. Marsupialia	17 (5 under 6 months in collection).
,,	10. Other Orders	0
		187 (48 under 6 months in collection).

TABLE 7

The infecting parasites identified from post mortem specimens.

	Mammalia	Aves	Reptilia	Batrachia	TOTAL
Cocci	9	7	0	0	16
Corynebacterium	4	1	0	0	5
Acid Fast	16	17	1	0	34
Pasteurella	3	1	0	0	4
Salmonella	5	6	1‡	0	12
Shigella	4	3	0	0	7
Coliforms, etc.	3	24	2	0	29
Brucella	0	0	0	0	0
Anaerobes	4	0	0	0	4
Spirochaetes	0	0	0	0	0
Actinomyces	6	0	0	0	6
Fungi	0	4	0	1	5
Viruses	4	0	0	0	4
Rickettsia and other organisms not specified	2	1*	0	0	3
Cestodes	3	2	7	0	12
Nematodes	2	6	17	2	27
Filaria	0	1	0	0	1
Trematodes	0	0	0	0	0
Other Worms	0	0	2	0	2
Sporozoa, etc.	0	0	0	0	0
Trypanosomes	0	0	0	0	0
Amoeba	0	0	0	0	0
Coccidia	0	0	0	0	0
Balantidium	0	0	0	0	0
Other Protozoa	1	0	1	0	2
Mites	2	2†	0	0	4
Ticks and Lice	0	0	0	0	0
Other Ecto-parasites	2	1	0	0	3
TOTAL	70	76	31	3	185

* Diamond Dove with Erysipelothrix infection of the brain.
† Air Sac Mites.
‡ Anaconda.

Amongst the specific causes of death, little need be specially mentioned. Under specific disease there was again no case of ornithosis during the entire year. The only specific disease which was troublesome was feline enteritis whose control in newly arrived animals is a matter of difficulty and concern.

Cases of Special Interest

No. 52/58. Golden Hamster. This was a case of death in a hamster apparently due to infection with trichomonas. The interest lies in the fact that trichomonas are usually numerous in the large gut of the hamster and are generally considered non-pathogenic. In this particular case numbers were so enormous that it was supposed that they must be the cause of an acute enteritis which caused the death of the animal.

TABLE 8

The infecting parasites amongst the main Orders of Mammalia.

	1	2	3	4	5	6	7	8	9	10	TOTAL
Cocci	8	0	4	0	4	0	6	0	0	0	22
Corynebacterium	0	0	0	0	1	0	5	0	0	0	6
Acid Fast	7	0	4	0	1	0	3	0	0	0	15
Pasteurella	0	0	0	1	1	0	3	0	0	0	5
Salmonella	0	0	3	0	3	0	0	0	1	0	7
Shigella	3	0	1	0	0	0	0	0	0	0	4
Coliforms, etc.	1	1	2	0	2	0	2	0	0	0	8
Brucella	0	0	0	0	0	0	0	0	0	0	0
Anaerobes	0	0	2	0	0	0	5	0	0	0	7
Spirochaetes	0	0	0	0	0	0	0	0	0	0	0
Actinomyces	0	0	1	0	0	0	2	0	3	0	6
Fungi	1	0	0	0	1	0	1	0	0	0	3
Viruses	0	0	4	0	0	0	0	0	0	0	4
Rickettsia and other organisms not specified	0	0	0	0	0	0	2	0	0	0	2
Cestodes	1	0	0	0	0	0	1	0	1	0	3
Nematodes	0	0	1	0	0	0	1	0	0	0	2
Filaria	0	0	0	0	0	0	0	0	0	0	0
Trematodes	0	0	0	0	0	0	0	0	0	0	0
Other Worms	0	0	0	0	0	0	0	0	0	0	0
Sporozoa, etc.	0	0	0	0	0	0	0	0	0	0	0
Trypanosomes	0	0	0	0	0	0	0	0	0	0	0
Amoeba	0	0	0	0	0	0	0	0	0	0	0
Coccidia	0	0	0	0	0	0	0	0	0	0	0
Balantidium	0	0	0	0	0	0	0	0	0	0	0
Other Protozoa	0	0	0	0	1	0	0	0	0	0	1
Mange Mites	0	0	0	0	2	0	0	0	0	0	2
Ticks and Lice	0	0	0	0	0	0	0	0	0	0	0
Other Ecto-parasites	0	0	1	0	0	0	0	0	1	0	2
TOTAL	21	1	23	1	16	0	31	0	6	0	99

Column 1. Primates ; 2. Insectivora ; 3. Carnivora ; 4. Pinnipedia ; 5. Rodentia and Lagomorpha ; 6. Perissodactyla ; 7. Artiodactyla ; 8. Edentata ; 9. Marsupialia ; 10. Other Orders.

No. 73/58. Short-tailed Wallaby : *No.* 130/58. Monteiro's Galago : *No.* 134/58 Dark Rat Kangaroo : *No.* 200/58. Three-banded Douroucouli. These four deaths were attributed to a condition of shock * and led to some interest being taken in this type of death amongst wild animals in captivity. The wallaby was one of a number in the cage which became involved in a fight. All the wallabies were involved except for the one which died. This one wallaby cowered in the corner while the fight was in progress and, when the fight was over, was dead. This case is of especial interest and importance

* This term is used as defined by Karsner, H. T. (1955) "Human Pathology", Eighth edition. Lippincott, Philadelphia and Montreal, pp. 101–103.

Vide also Smith, H. A. and Jones, T. C. (1957) "Veterinary Pathology", Henry Kimpton, London, pp. 148–153.

since it happened to be observed and the full facts are known. In the case of the dark rat kangaroo, the tail had been eaten away by the companions and a condition of typical shock had developed. The Monteiro's galago had also had its tail eaten by companions and this again went into a shocked state and was sick for about 24 hours before death occurred. The three-banded douroucouli was persecuted by a cage mate, a squirrel monkey, which had gnawed through the skin of the scalp, exposing the cranium. She, too, went into a shocked state from which she died in spite of all efforts to save her.

A number of other cases have been studied during the year in which a condition of shock has been more or less predominant, and the post mortem findings have been studied. Further experimental work is projected on the causes and prevention.

No. 199/58. Lar Gibbon ('Juliet'). About six months prior to death this gibbon had been diagnosed as acutely infected with *Shigella sonnei*. She was treated and made an apparent recovery but was continually returning because of mild bouts of ill health for which she was treated. It was, however, not possible again to demonstrate the presence of shigella in stool samples. She collapsed one day and died suddenly. On post mortem she was found to have suffered from haemorrhage of the small intestine and *Shigella sonnei* was again isolated from this organ. This case is of some importance as demonstrating that shigellosis, at any rate of some primates, is not harmless when active symptoms are absent and that it may at any time flare up to cause fatal disease. It is often said that primates all carry shigella and that it is harmless. With this view it is impossible to agree. Shigellosis in its chronic stage is a disease of the small intestine and often difficult to diagnose from stool samples when relatively inactive. Sudden death, as in this animal also is characteristic and has been experienced in the case of other species of primates such as patas monkeys : it is invariably due to sudden haemorrhage from the wall of the small intestine.

No. 208/58. Lar Gibbon : *No.* 317/58. Stuhlmann's Monkey : *No.* 314/58. Uganda White-nosed Monkey. All these monkeys died of generalized tuberculosis of bovine origin.

No. 230/58. Ferret. The ferret died of generalized tuberculosis.

No. 262/58. Polar Bear ('Brumas'). The young polar bear, born at Regent's Park some eight years previously, died suddenly. Post mortem revealed the presence of chronic pyelo-nephritis which had resulted in generalized septicaemia. The condition was due to an unmixed infection with *Pseudomonas aeruginosa*, an organism which is coming to be recognized as of some considerable importance amongst captive animals. During the previous year was recorded the death of a manatee in precisely similar circumstances and with similar findings *post mortem* and similar symptoms. In the case of this bear a severe condition of the heart was discovered associated with thickening of the leaves of the bi-cuspid valve and with mitral stenosis.

No. 398/58. Polar Bear (' Ulla '). 'Brumas's' mate. This young male polar bear, died from a strange accident which had not occurred previously. He fell from the Mappin Terraces into the concrete ditch and two limbs were fractured, necessitating his destruction.

No. 305/58. Red Kangaroo : *No.* 499/58. Oribi. The red kangaroo died of generalized nocardiosis (*Actinomyces macropodidarum*) and the oribi died of actinomycosis of the jaw and pneumonia.

No. 337/58. Chimpanzee ' Bobo '. A young chimpanzee, ' Bobo ', died of meningo-encephalitis which resulted from extension of infection from the respiratory mucosa and nasal sinuses. The organism responsible appears to have been *Micrococcus tetragenus*.

No. 417/58. Patas Monkey. A very emaciated patas monkey died three days after receipt at Regent's Park. It was very anaemic and the trouble was diagnosed from blood smears as acute myeloid leukaemia.

No. 374/58 and *No.* 382/58. Malayan Palm Civet. Two palm civets died after one month at Regent's Park from infection with *Salmonella typhimurium*.

No. 355/58. Reticulated Giraffe. The giraffe, born eleven months previously, was destroyed because of a fracture of the left tibia. Examination of the skeleton revealed that it was suffering from an advanced degree of osteoporosis of the same type as had been described in the young lions, that is to say that there was rarefaction of the bones but without deformity and the lesion resembled those that are associated with Ca/P imbalance. This appears to have been an isolated case since no other cases of this nature have been encountered in the Society's animals, nor are they described in the literature.

No. 454/58. Wart Hog. The wart hog had been sick for some considerable time and had grown very thin although eating ravenously. Specimens had been submitted for examination but nothing positive could be found. On *post mortem* he was found to be suffering from tuberculosis of avian origin.

No. 234/58. Crested Myna. This bird had four adult filaria free in the body cavity in the kidney region.

No. 268/58. Orange-cheeked Waxbill. The waxbill died of enteritis, which was not associated with the bacteria usually found, but with infection by *Pseudomonas aeruginosa*, the same organism as described in polar bear ' Brumas '.

No. 308/58. Rufous-beaked Snake. This snake died of pneumonia and this, too, was associated with the presence of *Pseudomonas aeruginosa*.

No. 192/58. Golden-fronted Fruit Sucker. This bird died of septicaemia associated with the presence of *Shigella alkalescens* which was isolated from the spleen.

No. 167/58. Great Eagle Owl (' Jenny '). This owl died of mycosis of the liver. This is recorded because the liver is an unusual site for this infection to be found.

No. 206/58. Emperor Boa. This snake died of drowning. It apparently got its head into a small open water container, breathed in at the wrong moment thus swamping its lungs.

No. 600/58. Tiger (' Nassau '). This tiger which had been about a year in the collection and may have been two and a half years old, was affected with ' megacolon.' The colon was of immense size, resembling the inner tube of a motor car ; the organ was filled with dirty liquid and about three to four large handfulls of small knuckle bones. Examination of sections at various points of the gut failed to reveal any abnormality of the enteric plexuses but there was a congenital atrophy of the pyloric sphincter. The presence of a normal my-enteric plexus differentiates the condition from the congenital megacolon of Hirschprung's disease in Man.

No. 615/58. Angwantibo. The angwantibo died of impaction of the stomach which was filled solidly with its own hair.

No. 636/58. Black-footed Penguin. The death of this penguin resulted from encephalitis the cause of which could not be determined. Cultures were negative and blood smears and smears of spleen and bone marrow failed to show the presence of sporozoan parasites such as malaria. Sections taken from the brain showed vascular cuffing indicating the probability of a virus infection. The symptoms and signs were so typical of avian encephalitis that this is supposed to have caused death.

No. 634/58. Masai Ostrich. The ostrich died of impaction of the gut. The cause of this was tuberculosis of the alimentary tract.

No. 670/58. Chilean Flamingo. This flamingo died of pneumonia consequent on mycotic infection of the lungs.

RESEARCH

Paralytic disease of young lions

The studies of the paralytic disease in young lions undertaken in collaboration with O. Graham-Jones, M.R.C.V.S., the Veterinary Officer, were completed and a paper was presented to the Scientific Meeting of the Society in November, 1958. It was satisfactorily established that this was primarily a disease of the skeleton and associated with a low ratio of calcium to phosphorus in the diet. It had not been fully appreciated previously that lions do not consume bones to any great extent and that they therefore do not obtain supplies of lime from this source. Attempts to treat and to cure three young lions by correction of the calcium/phosphorus balance were successful in arresting the progress of the disease. Recovery was sufficiently complete for the animals to go back on exhibition. Following this work steps have been taken to reform the diet given to all Felidae and to supply extra calcium in addition to the mineral supplements which were previously provided. A noticeable improvement in the condition and alertness of the animals has followed these dietary changes.

Osteo-dystrophies in New World monkeys

Osteo-dystrophic conditions have been recognized in New World monkeys for many years. Hamerton described them in the Report of the Pathologist for 1933. The aetiology of the condition has never been properly studied and cause and prevention have not been determined. It has been sometimes supposed that this condition, which is frequently seen in marmosets, woolly monkeys and capuchins, is a true rickets but one that will not respond to therapy with vitamin D and calcium. It has also been described as Paget's disease and as von Recklinghausen's disease.

These diseases have been under investigation during the year and it has been established that they are of the nature of *osteo-dystrophia fibrosa cystica*. Investigations tend to show that the cause of the trouble is tubular nephritis of unknown origin sometimes associated with enlargement of the parathyroid glands. A detailed pathological investigation is now being undertaken in collaboration with Mr O. Graham-Jones and Professor Cunningham of the Royal College of Surgeons.

Studies on shock and "Stress syndrome"

Amongst "the cases of special interest" described were four in which death was attributed to shock. In one case, a short-tailed wallaby died suddenly as a result of fear. In three cases death occurred four to five days after the infliction of injuries which could hardly of themselves have been fatal. In addition to these four cases, for some time past, puzzling appearances have been noticed at *post mortem* which did not appear to fit in with the general pattern of the disease to which death was ascribed. In course of time, it came to be realized that these changes were associated with a condition of shock which, in many animals kept in zoological collections, could be an important if not a major component of the disease picture. In veterinary medicine shock is encountered in cause of trauma, haemorrhage or following operations. As a component of generalized disease or as a disease in its own right, it is not recognized and Selye's (1950) concepts in regard to "stress" and "adaptation" syndromes have hitherto had no part.* It is, therefore, of great interest to find cases of apparent shock, supposedly arising from "stressor" agents of one kind or another in captive animals, not used experimentally. Investigations during the year have not advanced beyond the stage of observation but experimental work has been planned, and it is hoped to pursue this in collaboration with scientists who are interested in the subject and who are able to assist with biochemical facilities lacking at these laboratories.

Cases of shock appear clinically to be associated with psychological causes, with trauma, or with the course of any disease of septicaemic, toxaemic or pyaemic nature. Death may be immediate or it may be delayed, the latter being more common. In delayed death, this may occur from two to five days after the onset of symptoms. The animal lies down in a listless condition taking no interest in life though strangely enough it may rouse itself to take

* Vide Smith & Jones (1957) loc. cit. who state "..., there is no evidence that "stress" as above described is of importance in veterinary medicine."

Selye, H. (1950. *The physiology and pathology of exposure to stress*. Montreal, Canada : Acta. Inc.

some food. If disturbed it may be aggressive, but as soon as it is left alone again it settles back into its previous state of torpor. Cases, in which this apparent syndrome has been seen, have occurred amongst certain of the primates is association with dysentery, pneumonia and trauma ; gibbons and baboons appear to be susceptible but no case has so far been encountered amongst chimpanzees. Galagos, in particular, appear to succumb very readily. Wallabies and many of the rodents, including chinchillas, appear also to be very susceptible.

On post mortem the lungs are seen to be collapsed and anaemic, usually with petechial haemorrhages into the alveoli. This may be accompanied by superficial emphysema. The collapse is thought to be due to loss of turgor in the vascular tree due to redistribution of blood supply. Often there is blood stained serous fluid in the chest cavity. The liver is seen to be in a state of extreme congestion affecting all veins including the central veins and the sinusoids. Macroscopically the liver may show the 'nutmeg' appearance usually associated with congestive heart failure. The spleen is sometimes congested The kidneys may or may not be affected but usually are greatly congested, the site of greatest congestion being the pelvis and medulla. The adrenal glands are occasionally of normal size ; sometimes they are enlarged and haemorrhages show through the capsule, on section a haemorrhagic condition throughout the cortex being found. In other cases, the adrenals have a shrunken appearance and the capsule, instead of being stretched, appears loose and yellowish grey in colour ; on section the four zones cannot be differentiated by the naked eye and yellowish pigment is absent from the cortex. A study of the histology of a large number of adrenals in these cases is being made and will be reported in greater detail in due course.

ACKNOWLEDGMENTS

As in the previous year, much assistance and mutual co-operation has been enjoyed from scientists interested in certain aspects of our work.

Dr Taylor and Dr Carpenter of the Public Health Laboratories, Colindale, have again given assistance in the identification of obscure enteric organisms. Dr Soltys of the School of Animal Pathology, Cambridge, has assisted over the typing of acid-fast organisms, and Dr Neal of the Wellcome Institute has again given invaluable assistance over research into the diagnosis and treatment of amoebiasis of snakes. Professor Cunningham of the Royal College of Surgeons has collaborated over osteodystrophic diseases of New World monkeys. Dr Morson, St. Mark's Hospital, has interested himself in conditions of the alimentary system.

Kidney specimens have been sent to Miss F. Stranack of the Portmouth Royal Infirmary, who has sent useful reports of the findings as a result of micro-dissection techniques. Mr Lancaster, of the Medical Research Establishment, Porton, has received specimens of lungs from birds and we are particularly indebted for a series of painstaking reports and for stained and unstained sections.

Dr Symons, of the Royal Free Hospital, has continued to study cardiac specimens, and Dr Humphrey Lloyd of the Middlesex has studied arteries.

For the helpful co-operation of all these persons, thanks is expressed.

NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

9th February 1960

Professor A. J. E. Cave, M.D., D.Sc., F.R.C.S., F.L.S., in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : NOVEMBER AND DECEMBER 1959, AND JANUARY 1960

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to The Zoological Society's Menagerie in London during the months of November and December 1959 and January 1960 were 232 in number, including some domestic animals. The following are of special interest :—A female Arabian oryx *Oryx leucoryx* presented by Mr C. W. Woolley ; Three Umnak Island Collared lemmings *Dicrostonyx groenlandicus stevensoni* Nelson presented by Dr K. Zimmerman ; a Black-and-white cobra *Naje melanoleuca* presented by Mr C. J. P. Ionides C.M.Z.S. ; a Red-winged Crested cuckoo *Clamator coromandus* (Linné), new to the collection, presented by Messrs G. H. and J. R. Newmark ; a Bornean Yellow-throated marten *Martes flavigula saba* Chason & Klös, new to the collection, presented by Dr K. C. Searle C.M.Z.S. and Mr D. A. Brameld ; a Huang's rat *Rattus huang* (Bonhote), new to the collection, presented by Dr K. C. Searle C.M.Z.S. ; a Hoolock gibbon *Hylobates hoolock* presented by Mr G. B. Eastmore ; a Tufted capuchin *Cebus apella* presented by the Rev. Paul Knudsen ; two de Brazza's monkeys *Cercopithecus neglectus* and two Agile Crested mangabeys *Cercocebus galeritus agilis* presented by Dr A. J. Haddow C.M.Z.S.; a pair of cacomistles *Bassaricus sumichrasti* (Saussure), new to the collection, two moose *Aleces alces* and five reindeer *Rangifer tarandus* received in exchange ; a female Golden eagle *Aquila chrysaëtos chrysaëtos* was presented by the Royal Zoological Society of Scotland and a male of the same species was received in exchange from the Zoological Gardens at Helsingfors ; a collection of North American terrapins which included three Yellow mud-terrapins *Kinosternon flavescens* (Agassiz) and two Gulf Coast Soft-shelled turtles *Amyda spinifera asper* (Agassiz) received in exchange from Mr J. Lee Settlemyre ; a female Reticulated giraffe *Giraffa camelopardalis reticulata* and a Squirrel-like flying phalanger *Petaurus norfolcensis*, a Senegal bush baby *Galago senegalensis*, two pumas *Felis concolor*, a Spotted deer *Axis axis*, born in the Menagerie ; a feline douroucouli *Aotes trivirgatus infulatus* was also born in the Menagerie ; it is the second breeding recorded for this species, the first birth having occurred in 1939. During the same period there were 63 additions to the Menagerie at Whipsnade Park including some domestic animals. The following are of special interest :— An Asiatic wild ass *Equus hemionus* received in exchange from Zoo Centre

Moscow ; two Humboldt's penguins *Spheniscus humboldti* and two Greater snow geese *Anser caerulescens atlanticus*, hatched in the Park ; three White-bearded gnus *Connochaetes taurinus albojubatus*, born in the Park.

The following communications were read and discussed :—

Dr VERNON A. HARRIS. On the locomotion of the mud-skipper *Periophthalmus koelreuteri* (Pallas) : Gobiidae. [To be published in the " Proceedings ".]

Professor H. R. HEWER and Dr K. M. BACKHOUSE. Grey seals breeding on Eilean nan Ron. [To be published in the " Proceedings ".]

Mr W. H. DAWBIN. Open boat whaling in the Pacific (Illustrated by a film).

8th March, 1960

Professor A. J. E. CAVE, M.D., D.Sc., F.R.C.S., F.L.S.,
in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : FEBRUARY 1960

By H. G. VEVERS, M.B.E., M.A., D.PHIL.

The registered additions to The Zoological Society's Menagerie in London during the month of February were 28 in number, including some domestic animals. The following are of special interest :—Seven pandas *Ailurus fulgens*, received in exchange ; a Californian sea lion *Zalophus californianus*, and two Black-necked storks *Xenorhynchus asiaticus*, purchased. During the same period there were 30 additions to the Menagerie at Whipsnade Park. The following are of special interest :—A male guanaco *Lama guanicoe* and a female Bactrian camel *Camelus bactrianus*, born in the Menagerie.

The following communications were read and discussed :—

Professor R. J. HARRISON, Professor W. HAMILTON and Dr B. A. YOUNG. The fine structure of foetal-maternal relationship in the placenta of Cervidae;

Dr E. ELKAN. Some interesting pathological cases in amphibians. [To be published in the " Proceedings ".]

Dr A. J. CAIN and Dr G. A. HARRISON. Phyletic weighting. [To be published in the " Proceedings ".]

12th April 1960

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.,
President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MARCH 1960

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to The Zoological Society's Menagerie in London during the month of March were 108 in number, including some domestic

animals. The following are of special interest :—A Ring-tailed lemur *Lemur catta* was presented by Mr D. D. Jones and one was born in the Menagerie ; a Hog deer *Axis porcinus* was born in the Menagerie ; a Mrs Wilson's tanager *Calospiza nigrocincta franciscae* (Lafresnaye), new to the collection, and two Madagascar weaver birds *Foudia madagascariensis* were presented by Messrs G. H. and J. R. Newmark ; a Heine's humming bird *Amazilia tzacatl jucunda* (Heine), new to the collection, was received in exchange ; a kea *Nestor notabilis* was deposited ; a Louisiana Milk snake *Lampropeltis doliata amaura* Cope, new to the collection, was purchased. During the same period there were 11 additions to the Menagerie at Whipsnade Park, apart from transfers from London. The following is of special interest :—A Lear's macaw *Anodorhynchus leari*, was deposited.

The following communications were read and discussed :—

Dr Barbara M. Gilchrist. Growth and form of the brine shrimp *Artemia salina* L. [To be published in the " Proceedings ".]

Mr P. H. Greenwood and Mr K. S. Thomson. The pectoral anatomy of *Pantodon buchholzi* Peters (a freshwater flying fish) and the related Osteoglossidae. [To be published in the " Proceedings ".]

Professor C. G. Sibley. Hybridization in the Red-eyed towhees of Mexico ; a study of the evolution of reproductive isolation in birds.

NOTICE

["Proceedings", Vol. 134, Part 1, was published on the 29th April, 1960.]

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